Notes on the anatomy and classification of ophidiiform fishes with particular reference to the abyssal genus *Acanthonus* Günther, 1878

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CONTENTS

SYNOPSIS. Although the dominant group of benthic deep-sea fishes, Ophidiiformes are virtually unknown anatomically. This study focuses on anatomical features of the abyssal genus *Acanthonus* a taxon which previous authors have considered specialised. Of *ca* 80 ophidioid and bythitoid genera, 36 have been utilised for comparative study. The characters investigated are those commented upon by previous authors and ones not previously described. Characters identified as synapomorphic are the hypertrophy of the RLA-PP (pelvic) nerves, divergence of the supraorbital trunk of the trigeminal nerve complex external to the trigeminal foramen, reduction and loss of epipleural ribs and posterior shift of the swimbladder. The distribution of these characters upholds the classification of Cohen & Nielsen (1978) with respect to the recognition of a monophyletic Brotulinae and Ophidiinae, but indicates that the Neobythitinae is paraphyletic with part (*Hypopleuron*) being the sister-group to other ophidioids and bythitoids and other parts being closely related to respectively, brotulines and aphyonids. The Bythitidae also appears non-monophyletic with respect to one genus, *Brosmophyciops* whose phylogenetic position is ambiguous. The majority of Neobythitinae and Bythitidae are considered as a monophyletic assemblage, the detailed relationships of which are yet to be ascertained. It is confirmed that *Acanthonus* possesses several autapomorphies, and synapomorphies which support Cohen & Nielsen's (1978) contention that its close relationship lies with *Tauredophidium* and *Xyelacyba*.

INTRODUCTION

Gosline (1953) noted the dearth of anatomical accounts of ophidiiform (brotulid) fishes, reiterated by Cohen (1974) and Cohen & Nielsen (1978). Nearly fifteen years on the situation remains almost the same; there is no broad comparative anatomical treatment of the group.
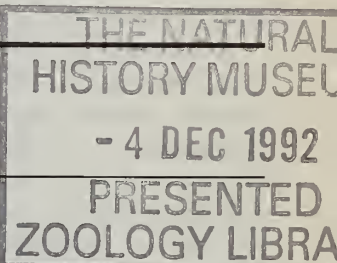
Gosline (1960) also drew attention to the size and heterogeneous nature of the group noting that 'known variation in osteological features in greater than between many families of . . . Percoidae'. In current systematic parlance this variation and heterogeneity can be attributed to an array of apomorphic features most of which appear to be autapomorphic at the generic 'level', witness the many (twenty-four among eighty-two [29%]) monotypic genera.

No attempt is made here to provide anything approaching a comprehensive anatomical survey of ophidiiform taxa, instead certain anatomical features are detailed from the standpoint of *Acanthonus*, a monotypic abyssal genus (Fig. 1). *Acanthonus* is presently placed in the majority ophidiiform group, the Neobythitinae; it appears to possess a number of specializations correlated with its abyssal life (Nielsen, 1966; Horn *et al.*, 1978) most of which appear to be unique but offering the possibility that some might be shared with anatomically uninvestigated taxa. It is these 'unique' features together with certain ophidiiform features commented upon by previous authors which are used as starting points in making a broader comparative anatomical investigation.

Regan (1903; 1912) and Gosline (1953) had made assertions concerning certain ophidiiform features and it is these which have been taken as a starting point for a broader comparative investigation. The taxonomic breadth of the comparisons is, however, limited by the availability of material. Among the *ca* eighty ophidioid and bythitoid genera, thirty-six (45%) have been used and then not for every character complex. By examining a combination of osteological, myological and neurological features it was hoped that synapomorphies would be revealed which would identify at least basal monophyletic assemblages. Thus far, only one potential synapomorphy, involving the morphology of the cranial articular facets and their connection with the vertebral column, has been recognised as splitting ophidiiforms into the Carapidae plus Ophidiidae and the Bythitoidei, the latter being the derived assemblage (Patterson & Rosen, 1989). Monophyly of the Carapidae has recently been satisfactorily demonstrated by Markle & Olney (1990) while that of both the Ophidiidae and Bythitoidei remains suspect.

METHODS AND MATERIALS

Although Patterson & Rosen (1989) recognised the Bythitoidei as a monophyletic group they were not explicit in the content of that group naming only certain genera lacking the synapomorphic 'cod-like' exoccipital facets and which were classed as 'ophidiids'. For the purposes of the anatomical descriptions the usage of 'ophidiiform(s)' embraces the Ophidoidei and Bythitoidei *sensu* Cohen & Nielsen (1978), the Carapidae being treated as an outgroup along with other paracanthopterygians.

Specimens examined (the majority have been dissected and radiographed and from some the cranium has been extracted): *Abyssobrotula galatheae* Nielsen Uncat. 'Discovery' Stn 10652, 5112 m (149 mm SL); *Acanthonus armatus* Gnthr 1990.8.21:78a–f (6 specs 290–350 mm SL), off Cape Verde, 3120 m; 1887.12.7.55 (holotype, 285 mm SL), Philippines; 1887.12.7.56 (Paratype, 310 mm SL) North of New Guinea; *Aphyonus gelatinosus* Gnthr 1887.12.7:59 (Holo-

type, 130 mm SL), N.E. Australia; *Barathrodemus cf. manatinus* Goode & Bean 1991.11.14.1 (107 mm SL), 24°25'N, 77°22'W; *Barathronus bicolor* Goode & Bean 1961.9.7:1 (104 mm SL), Puerto Rico; *Bathyonus* sp. Uncat. 'Discovery' Stn 12179 (190 mm SL); *Bassozetus taenia* (Gnthr) 1990.8.21:97–8 (205 mm SL, skull prep.), Cape Verde; *Bassozetus* sp. 1991.7.9:10–33 'Discovery' Stn 10884 (*ca* 156, 170 mm SL); *Brosmophyciops* sp. 1991.11.14:2 (52 mm SL) N.W. Gulf of Aqaba; *Brotula multibarbata* Temminck & Schlegel 1983.3.25:1128–30 (103 mm SL), Fiji; *Carapus acus* (Brunn.) 1952.11.25:1–4 (180 mm), Naples; *Carapus bermudensis* (Jones) 1985.6.6:138–183 (alizarin/alcian), Bimini; *Cataetyx* sp. 1990.8.21: 184–8 (226, 250 mm SL; skull prep.), Porcupine Seabight; *Cherublemma emmelas* (Gilbert) 1985.6.6:136–7 (205 mm SL), Baja California; *Dicrolene intronigra* Goode & Bean 1939.5.24:1441–4 (135 mm SL), S. Arabian coast; *Dinematichthys* sp. 1983.3.25:1123–5 (92 mm SL), Fiji; *Diplacanthopoma brachysoma* Gnthr 1972.10.24:4 (185 mm SL) 9°03'N, 81°18'W; *Echiodon drummondii* Thompson 1969.5.4:3–5 (300 mm SL) 58°N, 9°W; *Genypterus blacodes* (Schneider) 1936.8.26:1052–7 (290 mm SL) S. Atlantic; 1896.6.17:73, (skeleton) Melbourne Market; *Glyptophidium macropus* Alcock 1939.5.24:1458–65 (170 mm SL, skull prep.) Gulf of Aden; *Hoplobrotula armata* (Temminck & Schlegel) 1938.6.23:27–8 (193 mm SL), Chousi, Japan; *Hypopleuron caninum* Smith & Radcliffe 1986.10.6:63–65 (330 mm SL) Indonesia; *Lamprogrammus fragilis* Alcock 1939.5.24:1493–6 (130 mm, body truncated: 220 mm SL) S. Arabian coast; *L. niger* Alcock 1939.5.24:1483–7 (300 mm SL; skull ex *ca* 380 mm SL) maldive area; *Lepophidium profundorum* (Gill) 1984.8.8:263–6 (105 mm SL) Baja California; *Lucifuga dentatus* Poey 1981.10.27:1–4 (104 mm SL) Cuba; *Monomitopus metriostoma* (Vaillant) 1964.8.6:47–54 (135 mm SL) 7°55'N, 12°38'E; *Neobythites gilli* Goode & Bean 1967.11.9:1–6 (100 mm SL) Caribbean; *N. steatiticus* Alcock 1910.1.31:11 (skeleton) Sea of Oman; *Nybelinella erikssoni* (Nybelin) 1991.5.7:2 (58 mm SL) 'Discovery' Stn 11261, 5440 m; *Ogilbia cayorum* Evermann & Kendall 1985.6.6:128–135 (69, 72 mm SL) Bahamas; *Ophidion rochei* Muller 1971.12.17:6–8 (175 mm SL) and Uncat. (170 mm) Black Sea; *Penopus* sp (285 mm SL) 'Discovery' Stn 12177 (No. 2); *Petrotyx sanguineus* (Meek & Hildebrand) 1976.7.15:205 (410 mm SL) B.V.I.; *Porogadus trichiurus* (Alcock) 1939.5.24:1453–5 (175 mm SL) Zanzibar; *Pycnocraspedum squamipinne* Alcock 1939.5.24:1497–8 (114 mm SL) Zanzibar; *Sirembo imberis* (Temminck & Schlegel) 1905.2.4:450–4 (137 mm SL; skull prep.) Wakanoura, Japan; *Spectrunculus grandis* (Gnthr) Uncat. (125 mm SL, alcian stained spec.) 'Discovery' Stn 51015, 2540 m; 1990.8.21:106–111 (420; 250; 220 mm SL, skull prep) Porcupine Seabight; *Tauredophidium hextii* Alcock 1890.11.28:38 (type, 100 mm SL) Ganjam Coast; 1992.2.4:3–5 (89 mm SL) 11°31'S, 86°55'E; *Thalassobathia pelagica* Cohen 1967.11.8:1 (240 mm SL) Donegal; *Typhlonus nasus* Gnthr 1887.17.7:58 (Holotype, 205 mm, tail missing) N. of Celebes; 1887.12.7:587 (Paratype, 215 mm SL) N.E. of Australia; 1992.2.4:6 (190 mm SL) Indian ocean; *Xyelacyba myersi* Cohen USNM 320096 (120 mm SL) 24°51'N, 90°00'W; USNM 212087 (73 mm SL) 38°35'N, 72°23'W; 1992.2.4:1–2 (170 mm SL) 25°S, 88'E.

Pediculati: *Antenharius nummifer* (Cuvier) 1888.12.29:143 (skeleton); 1898.12.24:103–112 (49 mm SL) Persian Gulf; *Porichthys porosissimus* (Val.) 1937.9.30:163–7 Bahia Blanca; 1890.11.15:150 (skeleton); *Lophius piscatorius* Linn.

1970.2.17:630–2 (95 mm SL) S.W. Ireland; Uncat. (skull).

Abbreviations used in the figures

A1,2,a,b	Divisions of *adductor mandibulae* muscle
aa	anguloarticular
ahf	anterior hyomandibular fossa
asp	autosphenotic
bl	Baudelot's ligament
blf	fossa for attachment of Baudelot's ligament
bo	basioccipital
boc	basioccipital cavity for articulation with first centrum
bof	basioccipital facet
c	centrum (numbered)
c1p	anterior process of first centrum
cc	cerebellar corpus
cl	cleithrum
cle	cleithral extension
cs	spinal cord
de	dentary
do	*dilatator operculi* muscle
dRLA	dorsal branch of ramus accesorius lateralis nerve
dsp	dermosphenotic
ect	ectopterygoid
ent	entopterygoid
epd	dorsal epaxial muscle
epl	anterior lateral segment of *epaxialis* muscle
epm	anterior medial segment of *epaxialis* muscle
epo	epioccipital
epr	epipleural rib
eps	lateral band of epaxial muscle connecting 1st and 4th ribs
epx	epaxial muscle
es	ethmoid spine
exc	exoccipital condyle
exf	exoccipital facet
exo	exoccipital
fc	frontal crest
fg	foramen for glossopharyngeal nerve
fh	foramen for hyomandibularis nerve
fli	lateral ethmoid-first infraorbital facet
flp	lateral ethmoid-palatine facet (lateral)
fm	foramen magnum
fmp	lateral ethmoid-palatine facet (medial)
foo	foramen for optic-olfactory and trigeminal nerves
fon	foramen for occipital nerves
fr	frontal
fRLA	foramen for ramus lateralis accessorius nerve
fsn	spinal nerve foramen
ft	facial trunk of trigeminal nerve
fv	vagus nerve foramen
ga5	5th gill-arch
hb	hyoideus branch of hyomandibularis nerve
hy	hyomandibular
hyb2	2nd hypobranchial
hyx	hypaxial muscle
ic	intercalar
ica	*infracarinalis anterior* muscle
ih	interhyal
io	interoperculum
ki	kidney
lal	labial ligament
lap	*levator arcus palatini* muscle
lc	compound ligament
lcc	part of compound ligament connecting swimbladder with first rib
le	lateral ethmoid
lei	ethmoid-infraorbital ligament
li	liver
lin	interneural ligament
lmi	mandibular-interopercular ligament
lnr	neural-rib ligament
lo	*levator operculi* muscle
lpo	preopercular-opercular ligament
lpv	palato-vomerine ligament
lsv	swimbladder-vertebral ligament
mb	mandibular branch of hyomandibularis nerve
mbo	outer subbranch of above
me	mesethmoid
mec	ethmoid cartilage
med	medial opening of mandibular canal (dentary)
mt	metapterygoid
mx	maxilla
nI-X	cranial nerves
na1	first neural arch
na2	second neural arch
nad	auditory nerve
nmd	mandibular branch of trigeminal nerve
nmx	maxillary branch of trigeminal nerve
ns	neural spine
nv	vagus nerve
of	olfactory foramen
ofb	olfactory bulb
ofl	olfactory lobe
on	notch in lateral ethmoid for olfactory nerve
onp	perforation in orbital septum for olfactory nerve
op	operculum
opl	optic lobe
os	orbital septum
pal	palatine
pap	palatine prong
par	parietal
pb	pelvic bone
pce	*pharyngoclavicularis externus* muscle
pcl	postcleithrum
pe	peritoneum
ph	posterohyal
phy	*pharyngohyoideus* muscle
plr	pleural rib
pm	pelvic muscles
pmr	medial ridge of parasphenoid
pmx	premaxilla
ppf	posterior (pterotic) hyomandibular fossa
pr	pelvic fin ray
pro	prootic
ps	parasphenoid
psp	parasphenoid process
pte	pterotic
pts	pterosphenoid
ptt	posttemporal
q	quadrate
r1	first enlarged rib (pleural or epipleural)
r2,3	ribs (pleural or epipleural)
ra	retroarticular
rc	rostral cartilage
rd	*retractor dorsalis* muscle
rds	rostrodermosupraethmoid

RLA-PEL   pelvic branch of RLA nerve
RLA-PP   pectoral-pelvic branch of RLA nerve
rm   recti muscles
sb   swimbladder
sbc   sclerified cap of swimbladder
sh1   lateral segment of *sternohyoideus* muscle
shm   medial segment of *sternohyoideus* muscle
smx   supramaxilla
sn   spinal nerve
so   supraoccipital
sol   semi-ossified ligament
sop   suboperculum
sot   supraorbital trunk of trigeminal nerve
sp   sphenotic
ste   sclerified tunica externa of swimbladder
sy   symplectic
tepm   tendon of medial epaxial (swimbladder) muscle
ti   tunica interna
tnp   perforation in orbital septum for trigeminal trunk
uh   urohyal
ut   tendon-ligament connecting *sternohyoideus* with
           urohyal
vh   ventrohyal
vo   vomer
vps   vertebral parapophysis
vsr   ramus of third spinal nerve
vvp   vertebral ventral process

ANATOMICAL FEATURES

Ethmo-vomerine region and palatine

In *Acanthonus* the ossified dorsal surface of the ethmoid (rostrodermosupraethmoid, RDS) is produced anteriorly into a broad, dorsally channelled strut with a bifurcate tip which pierces the skin (Figs 1;2): this is the bifid spine referred to by Cohen & Nielsen, (1978:18). The posterior border of the RDS is only partially overlain by the frontals. The anterior surface of the underlying ethmoid is sharp-edged and overlies a thick ethmoid cartilage which is visible only laterally (emc, Fig. 2). The lateral ethmoid (le, Fig. 2) is broad with a sloped anterior face abutting the mesethmoid cartilage and a thin lateral wing. The ventrolateral surface of the lateral ethmoid bears a well-developed almost vertically directed medial (fmp) and a weak laterally directed articulatory process (flp, Fig. 2). These processes articulate respectively with the medial and anterior surfaces of the palatine prong. The medial part of the lateral ethmoid is deep and contacts the parasphenoid ventroposteriorly and the frontal dorsally. Each lateral ethmoid is separated from its partner in the midline. The olfactory foramen is variously developed. In the specimen illustrated the 'foramen' appears as a notch on the posterior rim of the lateral ethmoid wing. The olfactory nerve merely passes over the edge of the bone and crosses its anterior face to where the olfactory rosette is situated. In other specimens a thin posterior stem of bone provides either a complete or incomplete closure of the notch. The vomer (vo, Fig. 2) has a deep and broadly triangular head and a short narrow shaft the posterior tip of which lies in line with the posterior borders of the lateral ethmoids. The tooth-patch is deep and the conical teeth are directed not only ventrally but also anteriorly and anterodorsally (Fig. 2C).

The ethmovomerine region of *Acanthonus* differs most noticeably from the other ophidiiform taxa examined in three respects, 1) elongation and bifurcation of the RDS; 2) position of the palatine articulatory facets on the underside of the lateral ethmoid; 3) disposition of the vomerine teeth.

As in *Acanthonus* in nearly all other taxa the anterior of the mesethmoid capping the ethmoid cartilage slopes forward. However, the slope is variable from being almost vertical (*Ophidion* and *Genypterus*; Fig. 3A) to shallowly sloped (*Cataetyx* and *Lamprogrammus*; Fig. 3F). In *Glyptophydium*
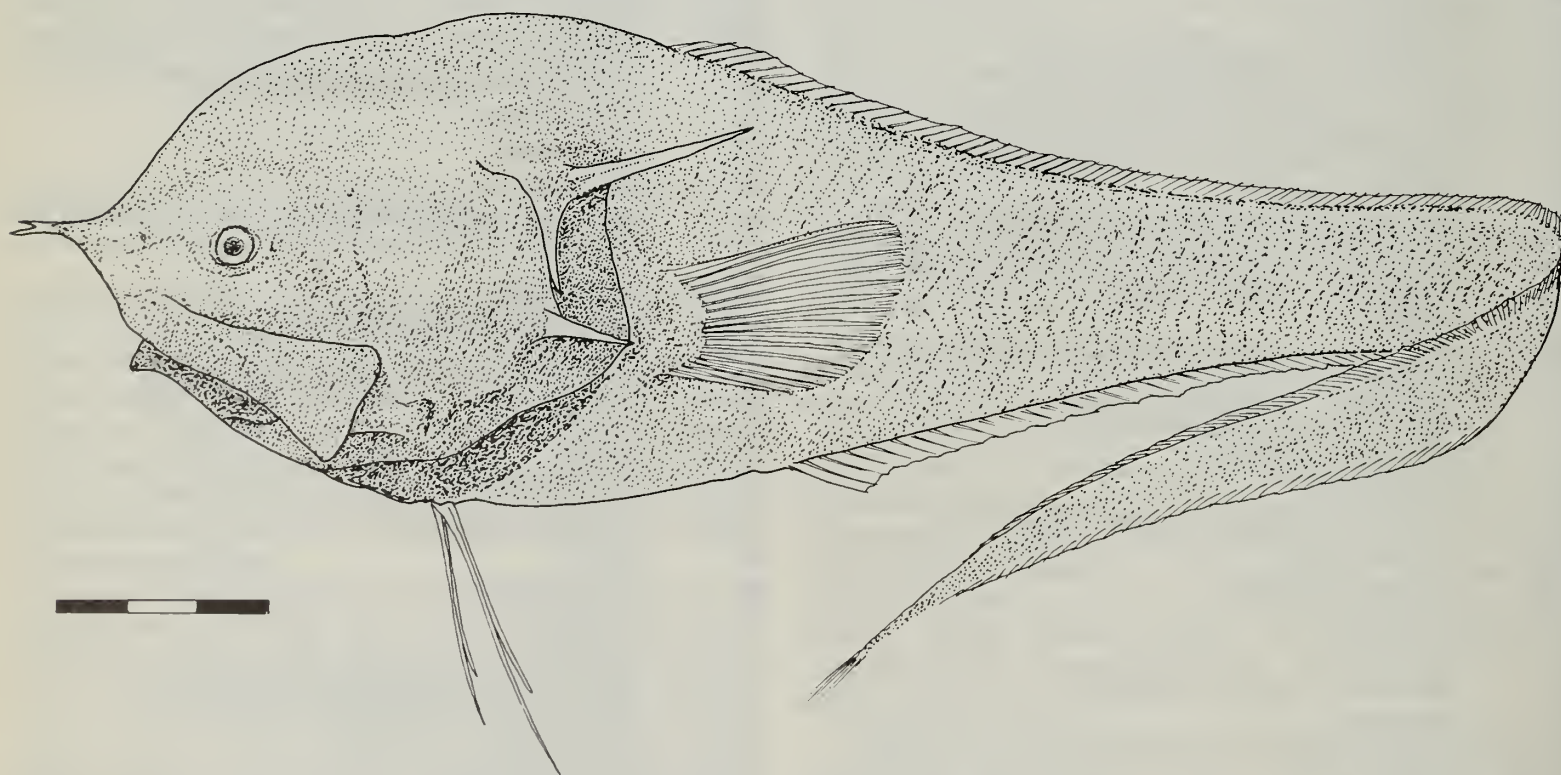

Fig. 1   *Acanthonus armatus*, life appearance based on type specimens, photograph in Horn *et al.* (1978) and Winther's drawing in Nielsen (1966). Scale in cms.
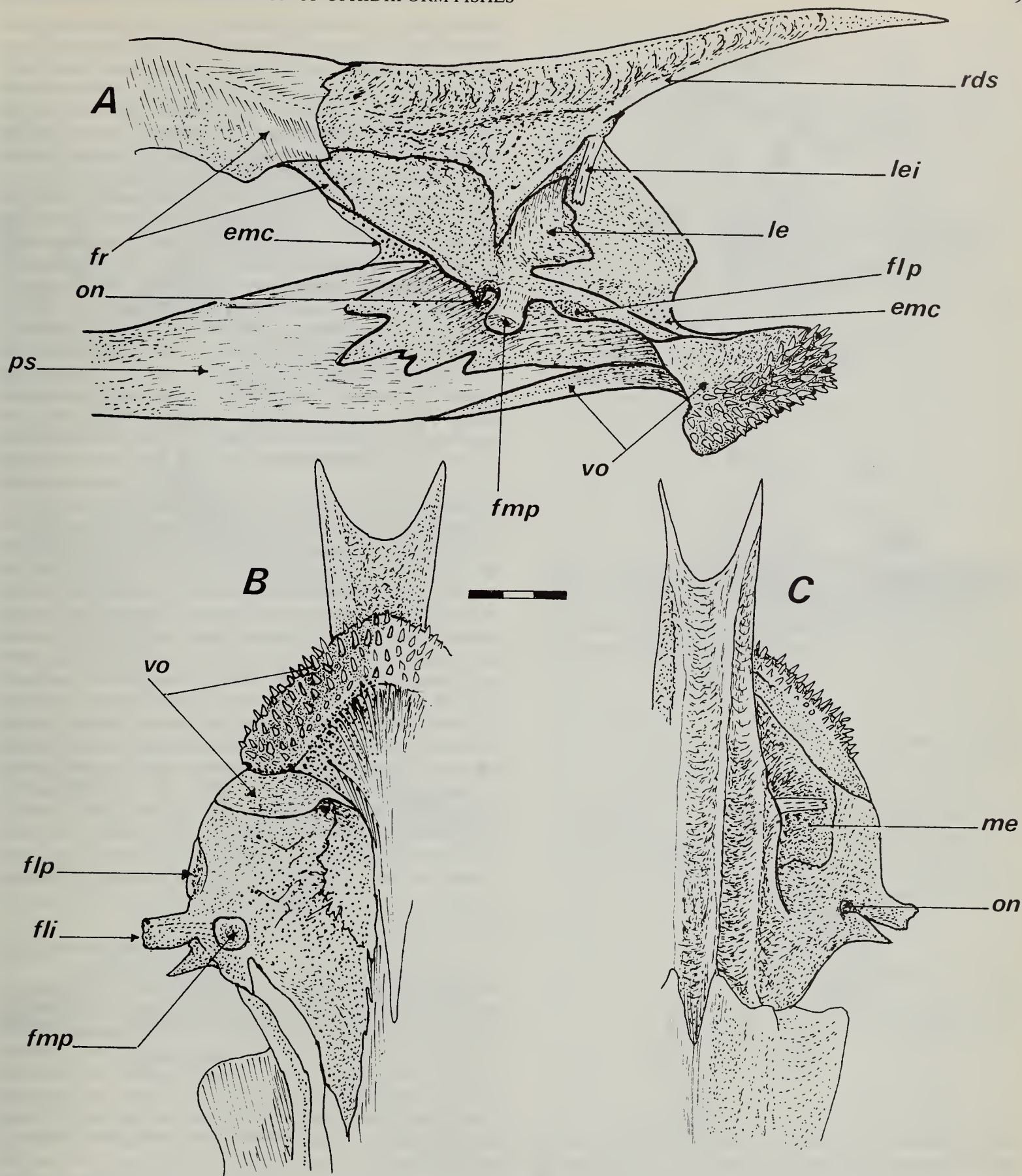
Fig. 2 *Acanthonus armatus* ethmovomerine region in A, lateral, B, ventral and C, dorsal views. Scale in this and subsequent figures in mm divisions.

(Fig. 3C), *Sirembo* and *Spectrunculus* the ethmoid region is indented and, notably in the latter genus, the frontals extend far anteriorly rising medially to form a crest which in *Glyptophidium* (Fig. 3C) is particularly pronounced. *Hoplobrotula* and *Tauredophidium* are the only other taxa examined which possess an anteriorly extended RDS spine (also reported by Machida, 1990). Only *Cataetyx, Brotula, Glyptophidium* and

Lamprogrammus have a prominent lateral wing on the lateral ethmoid. In other taxa, including *Acanthonus*, the wing is feebly developed but always has a lateral facet which articulates with the first infraorbital (fli, Fig. 3).

The disposition of the palatine articulatory facets on the lateral ethmoid is a variable and perhaps important classificatory feature. Unlike the condition in *Acanthonus* where the
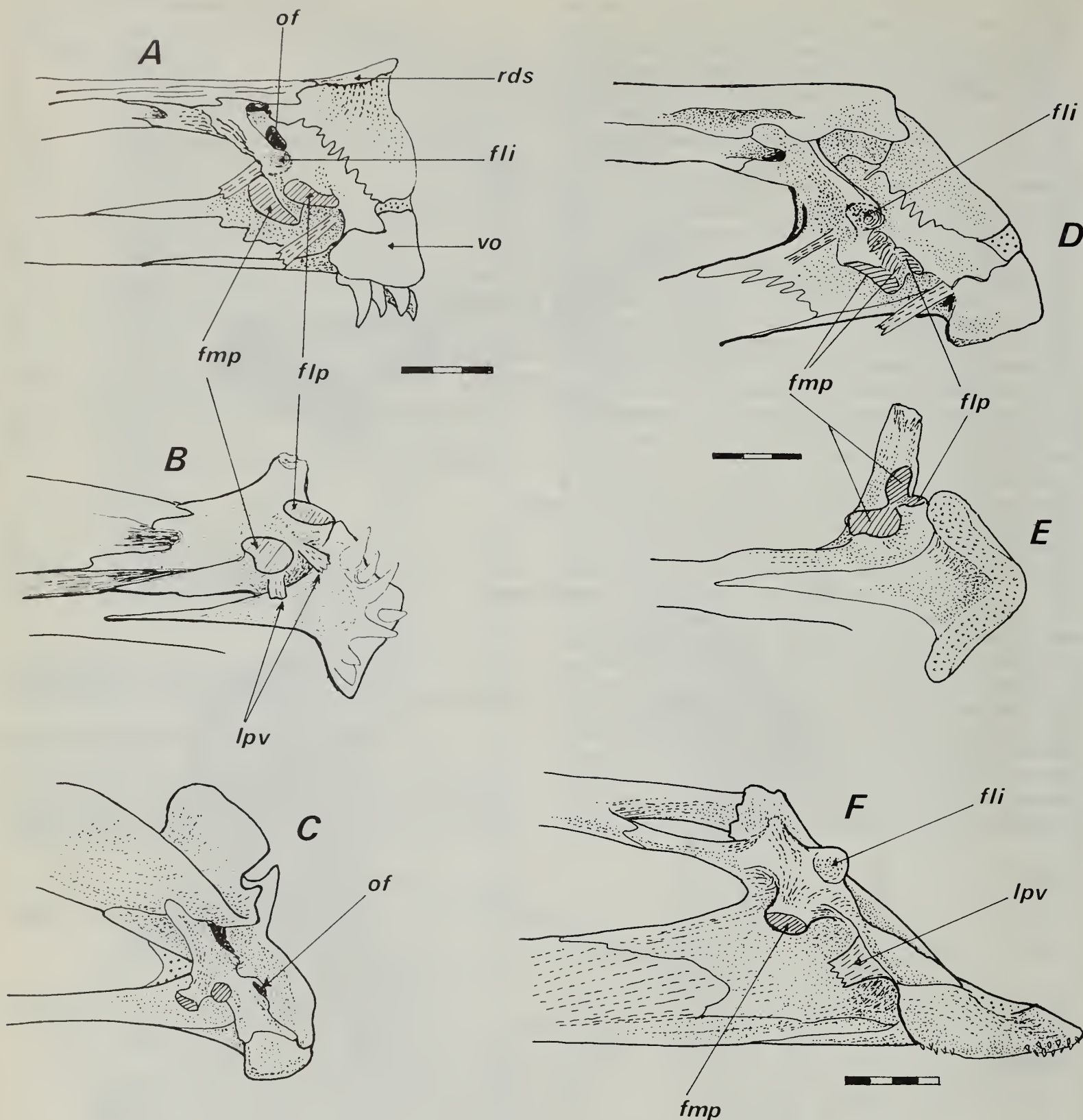
Fig. 3   Ethmovomerine regions of A and B *Genypterus blacodes* in lateral and ventral views; C, *Glyptophidium macropus* (lateral); *Brotula multibarbata* in D, lateral and E, ventral views; F, *Lamprogrammus niger* (lateral).

lateral facet is reduced, in other taxa examined both facets are equally well-developed. In *Brotula* (Fig. 3D,E), *Genypterus* (Fig. 3A), *Ophidion, Bassozetus, Glyptophidium* (Fig. 3C) and *Spectrunculus* the medial facet is large and ventroposteriorly directed and the outer facet is usually narrowly but clearly separated by a well-defined depression (exceptionally in *Brotula* the outer facet is juxtaposed to the inner and is continued on to the lateral flange of the lateral ethmoid; Fig. 3E). The lateral facet lies on the outer rim of the lateral ethmoid and is angled downward. The facets

contact apposing surfaces on the palatine head, the medial articulating with the dorsomedial surface of the head, the lateral with the base of the palatine prong. In *Lamprogrammus* there is only a medial facet, the base of the palatine prong being attached to the lateral ethmoid rim by a thick ligament (Fig. 3F). In *Cataetyx* the facets lie in an almost straight line but are well-separated.

The palatine-lateral ethmoid articulation in *Acanthonus* is rigid and the leading edge of the palatine is tightly juxtaposed to the vomer so that the vomerine and palatine teeth are

contiguous (Fig. 4B). A particular feature of the palatine teeth in *Acanthonus* is their lateral placement (Fig. 4B); in all other taxa examined the tooth patch is orientated along the medial surface of the bone so that nearly all the teeth point inward and only a single row is usually visible along the ventral margin of the bone. The palatine is secured to the lateral ethmoid by two ligaments (present in all taxa examined), one running from the dorsal indentation of the head of the bone or its medial rim to the lateral ethmoid wall, the other, which may sometimes be divided, from the inner face of the palatine prong to the lateral ethmoid cavity above the vomer (1pv, Fig. 3B). The latter ligament corresponds to Stiassny's (1986) anterior palato-vomerine ligament (VI). In all the taxa examined which embrace Cohen & Nielsen's (1978) brotulines, ophidines and neobythitines, this ligament invariably stems from the lateral ethmoid itself rather than the vomer. A medial palato-lateral ethmoid ligament is a widespread teleostean feature. There is, however, no posterior palato-vomerine ligament (Stiassny's ligament V) in any of the examined taxa. This absence is most likely a secondary loss associated with the development of lateral ethmoid-palatine articulatory facets.

The shape of the palatine, the angle at which the prong is directed and the proximity of the anterior palatine margin to the vomer are largely dictated by the orientation of the palatine facets with the corresponding articular surfaces of the lateral ethmoid. Usually the articulatory facets of the palatine are discrete, the medial one forming a right-angle to that on the neck of the prong so that the base of the prong lies in the saddle of the articulatory processes. As noted above, in *Cataetyx* the articulatory facets on the lateral ethmoid lie nearly in tandem, consequently the palatine prong extends directly forward rather than pointing ventrolaterally and the anterior lateral ethmoid facet appears to act as a stay. In its rigidity with the lateral ethmoid and juxtaposition with the posterior rim of the vomer, the palatine articulation of *Cataetyx* most closely approaches that of *Acanthonus* (Fig. 4A). There are, however, noticeable differences between the two taxa in the angle of the palatine prong and shape of articulatory surfaces which suggest that the resemblances have been independently derived.

Palatine-lower jaw bite

The reason for the rigidity of the palatine-ethmovomerine connection in *Acanthonus* becomes clear when it is realised that the palatine occludes with the lower jaw (Fig. 4B). The palatine tooth patch is long, 75% of the dentary and when occluded the posterior tips of the palatine and dentary tooth-patches coincide (Fig. 4B). In other ophidiiforms (and indeed, other teleosts) there is no or only partial (see below) occlusion between the palatine and lower jaw; the length of the palatine tooth patch is usually only half that of the dentary and the teeth are angled medially and fall inside the lower jaw when the mouth is closed so that teeth are rarely visible in lateral view (Fig. 5C). To what extent, in life, the palatine can be rotated laterally so as to occlude with the lower jaw is not clear merely from the manipulation of the jaws of preserved specimens but certainly the connection between the palatine and ethmovomerine region is loose enough to allow some lateral rotation.

Of the four exceptions among examined taxa two display partial and two (apparently) complete occlusion between the palatine and dentary. In *Lamprogrammus* and *Spectrunculus*
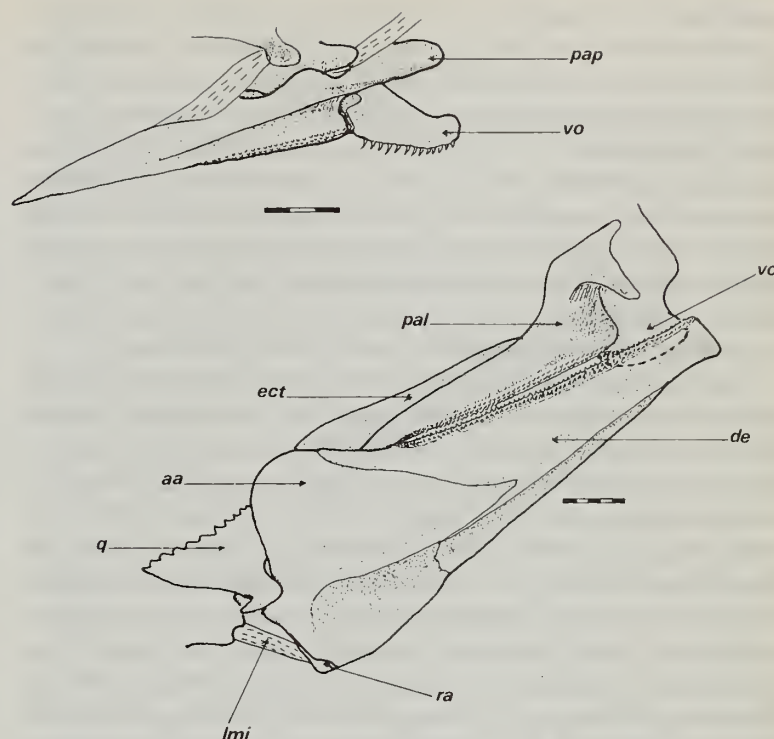

Fig. 4 Above, palatine and vomer of *Cataetyx* sp. (right lateral); below, palatine-lower jaw occlusion in *Acanthonus armatus*; the lower jaw is shown in the closed position and the elements are orientated with respect to the vertebral axis. Dashed outline indicates hidden border of the vomer.
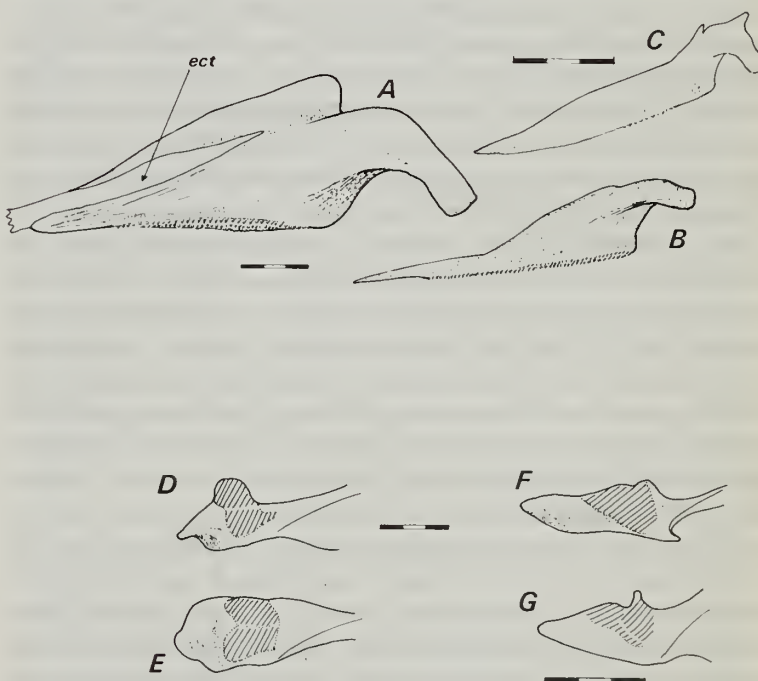

Fig. 5 Above, palatines of A, *Lamprogrammus niger*, B, *Spectrunculus grandis*, C, *Neobythites steatiticus* (right lateral views). Below, articulatory surfaces of lower jaws of D, *Acanthonus armatus*, E, *Lamprogrammus niger*, F, *Genypterus blacodes*, G, *Spectrunculus grandis* (dorsal view, medial surface at top).

only the posterior half of the palatine is in direct contact with the lower jaw when the mouth is tightly shut, the anterior half curving medially. The dentigerous surface of the palatine in *Spectrunculus* is longer than that of other taxa (Fig. 5B) but

nonetheless its posterior tip extends backward beyond the posterior tip of the dentary tooth patch, a feature common to all other genera examined. In both *Lamprogrammus* and *Spectrunculus* the palatine dentigerous area is exposed laterally (Figs 5A & B). From radiographs and partial dissections of *Tauredophidium* and *Xyelacyba* it would seem that these taxa also have complete or nearly complete occlusion of the palatine and lower jaw. In *Xyelacyba* the palatine is deep with a strong and steeply angled prong (as in *Acanthonus*) and in both *Tauredophidium* and *Xyelacyba* the palatine tooth patch is narrow with the teeth laterally exposed.

Acanthonus is not unusual among ophidiiforms in lacking upper and lower jaw occlusion, indeed it seems to be the common condition among this group of fishes that the lower jaw is surrounded by the upper when the mouth is shut. The feature is most clearly seen in *Spectrunculus* where the rather sharp-edged lip of the lower jaw forms a tight seal with the overlapping upper lip. *Typhlonus* is unusual among ophidiiforms in possessing long premaxillary ascending processes which also allow the upper jaw to envelope the lower. The dentigerous surface of the upper jaw rarely contacts that of the lower although in *Cataetyx* the tooth bands contact one another anteriorly. In *Lamprogrammus* there is a prominent dentary symphyseal process which lodges in a symphyseal notch in the upper jaw and although *Acanthonus* also bears a similar dentary process it is completely covered when the upper jaw is closed.

Quadrate-preopercular modification

The occlusion between the palatine and lower jaw teeth in *Acanthonus* is allowed principally by modifications in the relationship of the quadrate to the lower jaw and the contact between the quadrate and preoperculum. *Acanthonus* differs principally from other taxa examined in having the quadrate outwardly curved and the arc of that curvature continued through the ectopterygoid thus considerably displacing the palatine laterally (Fig. 6). In other ophidiiform taxa the anterior border of the quadrate is either perpendicular or inwardly curved so that the palatine lies either in the same vertical plane as the quadrate condyle or only slightly laterally (Fig. 6). Only in *Spectrunculus* is there a noticeable outward curvature of the quadrate and lateral displacement of the palatine. The shape of the *Acanthonus* quadrate condyle shows no special modification although it is somewhat shallower and its medial face more attenuated ventromedially than that of other taxa (Fig. 6).

When the lower jaws of various taxa are positioned at the same angle with respect to the quadrate it is seen that in *Acanthonus* the upper anterior face of the bone and the lower border of the ectopterygoid are obscured laterally by the anguloarticular; in the other taxa, there is a wide separation between the quadrate-ectopterygoid border. Only *Lamprogrammus* approaches *Acanthonus* in the separation of the elements (radiographs of *Tauredophidium* indicate a similar condition). *Acanthonus* and *Lamprogrammus* also possess a similarly modified anguloarticular condyle and its shape possibly dictates the alignment of the lower jaw (the condition in *Tauredophidium* is unknown). In the majority of ophidiiform taxa examined the anguloarticular is elongated, terminating in a posteriorly directed pointed or rounded process (Figs 5F & G). The transverse saddle of the condyle is well defined and the articulatory surface is elongate and extends on to the medial side of the condyle. In contrast both

Acanthonus and *Lamprogrammus* have a short articulatory condyle with an angled, slightly upturned blunt posterior process and there is a well-defined saddle with articulatory facets equally or nearly equally disposed on either side (Figs 5D & E).

The articulation between the ventral surface of the quadrate and the lower limb of the preoperculum in *Acanthonus* is absent in the majority of other taxa examined. The posteroventral surface of the quadrate is flared and sits across a similarly widened preopercular flange (Fig. 7). A preopercular flange, which extends ventrally to cover the neuromasts, is common to all the taxa examined but in *Acanthonus* it extends shelf-like from the bone and terminates in a ventrally extended triangular process (Fig. 7). *Lamprogrammus* and *Xyelacyba* also have a broad based quadrate and an extended preopercular lateral flange (radiographs of *Tauredophidium* indicate a similar condition). In *Lamprogrammus*, however, the flange does not turn ventrally but extends laterally well beyond the quadrate border. *Acanthonus* differs from all these taxa in that it is only the posterior half of the quadrate which contacts the preopercular limb. In the others nearly the entire quadrate lies on the preopercular limb so that its anterior tip comes close to the quadrate condyle.

In *Acanthonus* the preoperculum has a slender upright limb which has a slight anterior ridge and a short horizontal limb (Fig. 7). In addition to the lateral ventral spine (see above) the posteroventral border is also produced into a long stout spine. In other examined taxa there are two principal conditions of the preopercular upright limb, it is either slender as in *Acanthonus* or short and broad with a rounded posteroventral margin. In those six taxa with a slender limb, five (*Neobythites*, *Hoplobrotula*, *Monomitopus*, *Dicrolene* and *Tauredophidium*) have the posteroventral border developed into two or three spines. *Tauredophidium* has especially long spines similar to those of *Acanthonus*. *Brotula* lacks preopercular spines and most of the lateral face of the upright limb is covered by a pronounced flange; the horizontal limb is also elongated and modified (see p. 122). Of those taxa with short, rounded upright preopercular limbs none bear spines but an anterior groove and flange is often present. In the taxa with a slender preopercular limb neuromasts are poorly developed but in those with a short limb are either moderately or well-developed (*Lamprogrammus*, *Dicrolene*, *Monomitopus*) or absent (*Genypterus*, *Cataetyx*).

A particular feature of *Acanthonus* is a ligament which stretches from the posterodorsal rim of the preoperculum across the hyomandibular articulation to the anteroventral margin of the operculum (lpo, Fig. 17); this feature is otherwise present only in *Tauredophidium* and *Xyelacyba*. In *Typhlonus* a strong ligament extends from a groove in the centre of the lateral face of the preoperculum to insert on the lower articulatory margin of the operculum and does not extend across it.

Hyomandibular articulation and foramina

In *Acanthonus* the hyomandibular is short, lacks a pronounced stem and has a slightly indented anterior margin and a short opercular articular process (hy, Fig. 7). The posterodorsal part of the bone has an acute mesad slope so that the perpendicular plane of the body and stem of the bone comes to lie at some distance lateral to its articulation with the cranium. The posterior half of the dorsal border of the hyomandibular curves sharply mesad so that the posterior
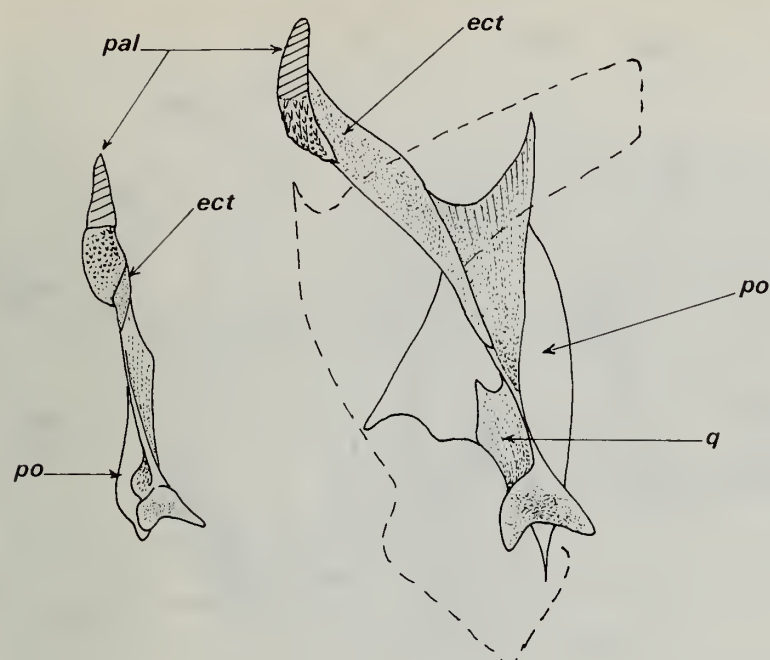
Fig. 6 Palato-pterygoid orientation right side, viewed anteriorly, in *Acanthonus armatus* (right) and *Neobythites steatiticus* (left). The anterior part of the palatine has been cut through (hatched). The position of the lower jaw in *Acanthonus* is shown by a dashed line.
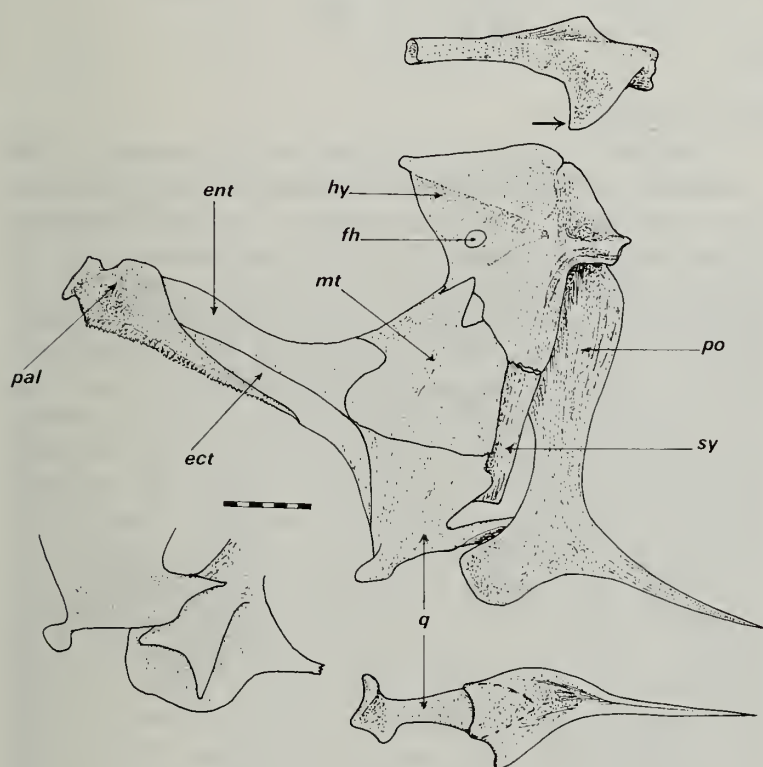

Fig. 7 *Acanthonus armatus*; hyomandibular and palato-pterygoid series, right side, in medial view (main figure); above, dorsal view of hyomandibular, medial surface to the bottom, the arrow indicates the surface articulating with the pterotic; below, ventral view of quadrate and preoperculum (dashed line shows shape of quadrate base), lateral surface at top; below left, lateral view of quadrate showing its contact with the preoperculum.

articulation is with a shallow fossa which curves around the posterior border of the pterotic and terminates in a notch (ppf, Fig. 8). The anterior articulation is with a deep fossa on the posterior surface of the sphenotic. The anterior fossa extends posteriorly as a shallow groove a short way along the

pterotic and is widely separated from the posterior fossa (ahf, Fig. 8).

The foramen for the hyomandibular trunk of the facial (VII) nerve lies in the centre of the anterior field of the bone and the nerve passes directly through it to immediately turn ventrad on the lateral face. In no other ophidiiform taxon examined does the upper part of the hyomandibular curve mesad as in *Acanthonus* and in only three genera (*Spectrunculus, Bathyonus, Bassozetus*) is the nerve foramen situated in the anterior field. In other taxa the foramen perforates the dorsoanterior strut of the bone. The nerve enters a medial opening and courses posteroventrally through the strut to exit from a lateral opening situated at a lower level than the medial (Figs 9B & C). Markle & Olney (1990) report that in *Brotula multibarbata* the hyomandibular foramen is small and located close to the edge of the bone. Furthermore, they note two conditions of the foramen in carapids whereby it either pierces the anterior strut or the area below the strut. These conditions correspond to the two states observed in ophidioids. Markle & Olney's observation of a small, anteriorly located foramen in *Brotula* is either erroneous or based on an aberrant specimen (in their figure (24) the foramen seems too small to transmit the large diameter trunk of the hyomandibular nerve). As such their polarity assignment of a derived state to the larger carapid foramen is questionable.

A foramen piercing the hyomandibular anterior strut appears to be the widespread euteleostean condition since it occurs in virtually all of a wide range of taxa examined (clupeomorphs, ostariophysans, berycoids, atherinomorphs, percomorphs). Among other paracenthopterygians the hyomandibular has been modified to a greater or lesser extent with subsequent relocation of the foramen and nerve course. In gadiforms attrition of the anterior strut has resulted in the foramen appearing at the anterior margin of the hyomandibular rather than the medial face of the bone (Howes, 1989), a character which Gosline (1968) used to define Gadiformes. In the bathygadid *Gadomus* attrition of the anterior strut has led to complete absence of an anterior hyomandibular foramen, a feature also common to (?all) macrouroids (Howes, 1989, figs 8 & 9A). Interestingly, the absence of a dorsoanterior strut from the hyomandibular of *Acanthonus* suggests a direct correlation with the loss of the pars jugularis. In the pediculate paracanthopterygians examined (*Lophius, Antennarius, Porichthys*) the hyomandibular trunk travels through the central stem of the bone (Fig. 9A) and upon exiting *via* a lateral foramen at the base of the stem the hyoideus branch departs from the mandibularis branch. In gadiforms the hyoideus departs from the mandibularis prior to entering the hyomandibular and travels separately within or across the bone (Howes, 1989, Fig. 9). In ophidiiforms and other teleosts examined the hyoideus branch departs from the mandibularis immediately on leaving the foramen and crosses the lower face of the hyomandibular (Fig. 9C). *Brotula* is unique amongst the ophidiiforms examined in that the hyoideus branch runs interiorly through the stem of the hyomandibular before exiting posteroventrally (Fig. 9B).

The 'precursor' of the *Brotula* condition occurs in *Hoplobrotula* where a strong flange lies diagonally along the lateral face of the hyomandibular following the line of the central stem and partially covering the nerve. The conditions in *Brotula* and the pediculate paracanthopterygians are clearly not homologous since in the former only the hyoideus branch of the hyomandibular trunk runs internally and exits from a separate foramen. The Pediculati are derived with respect to
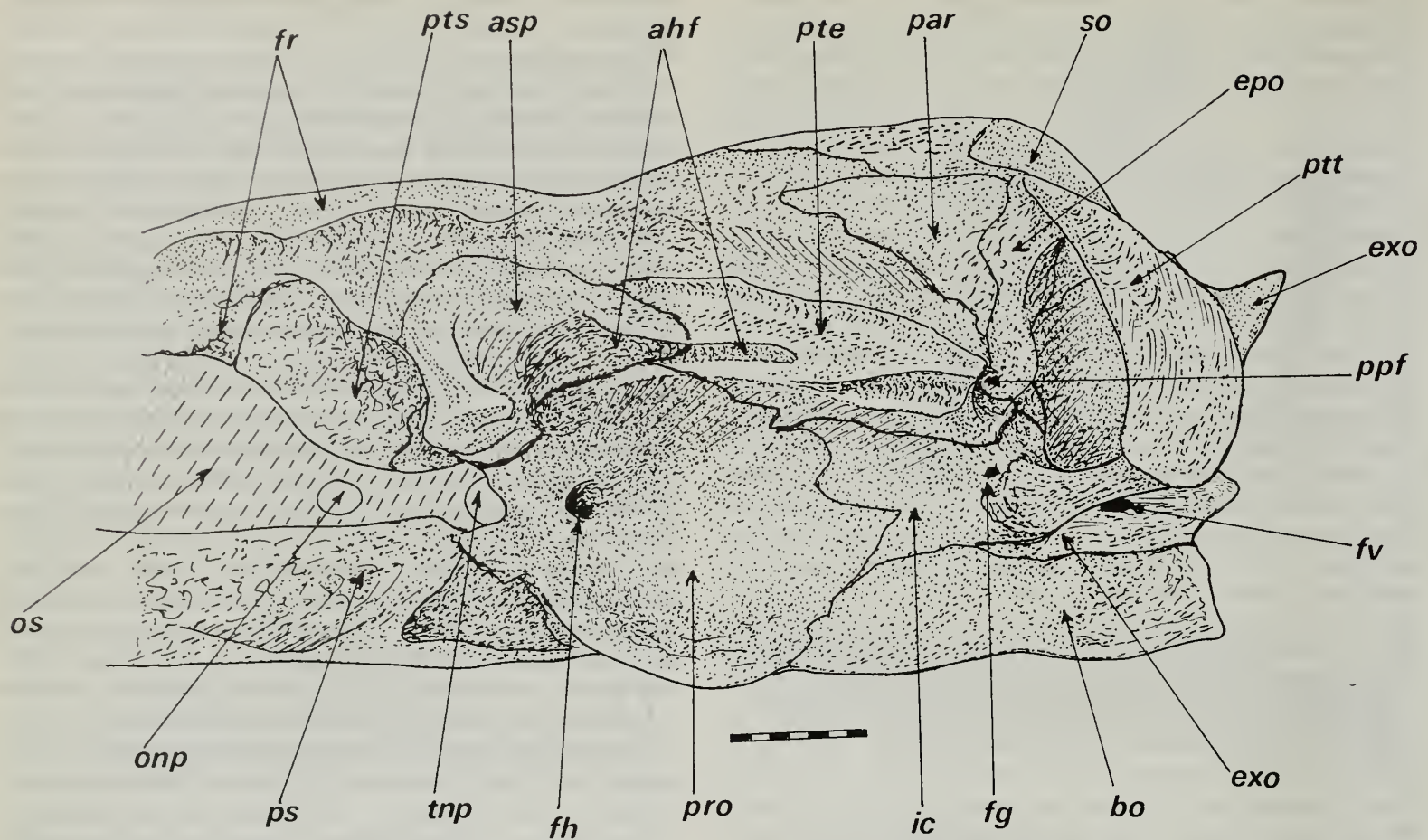
Fig. 8 *Acanthonus armatus* Neurocranium; postorbital and occipital regions in left lateral view.

other Gadoidei in the enclosed passage of the nerve through the hyomandibular. The majority of ophidiiforms possess a condition corresponding to that in other euteleosts where the nerve travels a short distance within the anterior strut of the hyomandibular. The transmission of the nerve directly through a foramen in the anterior lamina of the bone is considered derived in *Acanthonus* and *Spectrunculus*.

The hyomandibular opercular process in *Acanthonus* is short (Fig. 7), in which respect it is like that of a wide spectrum of taxa including Carapidae, *Hypopleuron*, *Glyptophidium*, *Tauredophidium* and *Brotula* (Fig. 9B). Among other taxa, however, the process is long (*Neobythites*, *Sirembo*, *Monomitopus*, *Genypterus*, *Ophidion*) and is especially so in *Spectrunculus*, *Cataetyx* and *Bathyonus*.

Trigeminal nerve foramina and nerve courses

In *Acanthonus* the trigeminal, facial, optic and olfactory nerves exit the cranium through a common aperture. However, they pass through separate openings in a membranous septum which extends between the pterosphenoid-prootic and parasphenoid (Fig. 8). In having a common cranial nerve foramen *Acanthonus* differs from all other ophidiiforms examined (with the exception of *Bassozetus*, *Abyssobrotula* and *Lucifuga*); among those other taxa are major differences in the arrangement of the trigeminal-facialis foramina.

A narrow prootic lateral commissure is common to all the examined taxa with the exception of *Genypterus* and *Cataetyx*, both of which have a long lateral commissure (Fig. 10A). In all taxa the hyomandibular trunk foramen is narrowly separated from the trigeminal but the distance between the trigeminal foramen and opticolfactory aperture

is variable. In *Genypterus* the distance is greatly increased due to elongation of the parasphenoid ascending process and pterosphenoid. In *Brotula* (Fig. 10C), *Spectrunculus* and *Cataetyx* the distance between the foramina is half that in *Genypterus* whereas in *Glyptophidium*, *Neobythites* (Fig. 10B), *Sirembo* and *Monomitopus* the separation is narrow. In *Lamprogrammus* it is intermediate between the first and second group of taxa. *Bassozetus*, *Abyssobrotula* and *Lucifuga* resemble *Acanthonus* in lacking a separate trigeminal foramen and in all these genera the common cranial nerve foramen is bordered by a lateral commissure. The size of the common cranial nerve foramen is variable but in *Brotula*, *Sirembo* and *Genypterus* it is narrow, exceptionally so in *Brotula* (foo, Fig. 10C) where an anteriorly directed laminar process rises from the midline of the parasphenoid and serves to separate the nerve tracts of either side (psp, Fig. 10C). According to Markle & Olney (1990) this process is a basisphenoid. However, in my specimen there is no suture to indicate that it is a separate element and the process stems from a medial ridge along the parasphenoid (pmr, Fig. 10C). In *Neobythites* the parasphenoid bears prominent paired ridges (pmr, Fig. 10B) but lacks a medial process. A basisphenoid does not occur in any ophidiiform or gadiform examined.

In *Acanthonus* the supraorbital trunk of the trigeminal nerve complex diverges from the infraorbital trunk at the point of emergence of the nerve bundle from the common cranial nerve foramen (Fig. 11). The RLA branch of the supraorbital (not shown in figure) extends dorsad entering a foramen between the sphenotic and pterosphenoid to pass caudad beneath the sphenotic and pterotic bones.

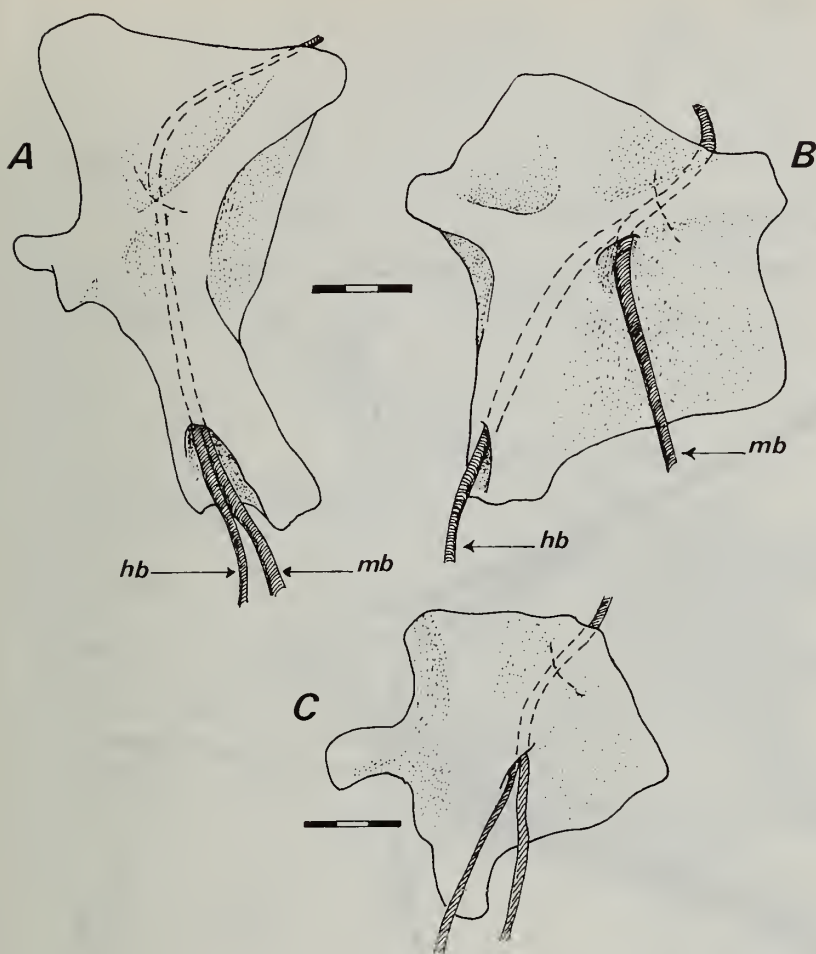Among other ophidiids, bythitids and aphyonids examined

Fig. 9 Hyomandibular and its nerve courses in A, *Porichthys porosissimus*, B, *Brotula multibarbata*, C, *Neobythites gilli* (right lateral views).

two groups of genera can be distinguished on the basis of whether the supraorbital trunk branches from the infraorbital trunk external or internal to the facialis chamber in the prootic. In *Brotula, Genypterus, Parophidium, Cherublemma, Ophidion* (Group A, Table 1) (Figs 12E & F), branching occurs within the chamber, the supraorbital nerves departing from the cranial cavity through separate foramina, as is the usual condition in teleosts (Fig. 12E). In *Dicrolene, Hoplobrotula, Sirembo* and *Neobythites* branching occurs at the point of emergence and the supraorbital nerves run dorsad along a channel in the outer surface of the sphenotic (Fig. 12A). In all other examined taxa (Group B, Table 1) branching occurs external to the chamber whether or not the exit foramen is common to the optic and olfactory nerves as in *Acanthonus, Bassozetus* (Fig. 12D), *Abyssobrotula* and *Lucifuga* or a separate trigeminal foramen as in the other above-cited genera (Fig. 12B, C & F).

Among gadoids and macrouroids the supraorbital nerves branch from the trigeminal trunk just prior to the latter's exit from the common optic-trigeminal foramen. The nerves then run medial to the pterosphenoid, departing from the cranial cavity *via* a foramen between the pterosphenoid and frontal to lie against the roof of the orbital cavity.

Branching of the supraorbital nerves external to the cranial cavity and lack of separate formina are considered derived conditions. The situation in *Hoplobrotula, Sirembo* and *Dicrolene* where marginal branching exists but a channel serves to conduct the supraorbital nerves dorsally is hypothesised to be a condition intermediate with the external branching and
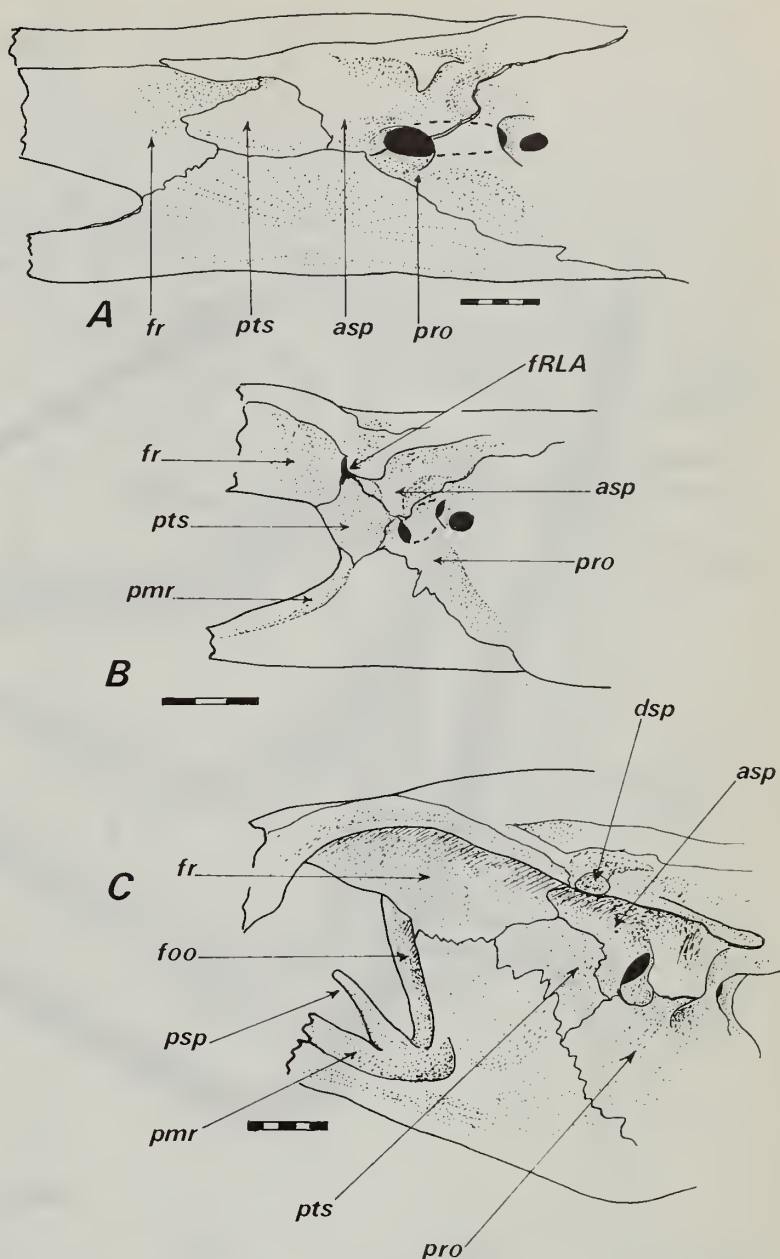

Fig. 10 Postorbital connections in A, *Genypterus blacodes*, B, *Neobythites steatiticus*, C, *Brotula multibarbata* (left lateral views). The extent of the trigeminal foramen covered by the lateral commissure of the prootic is indicated by dashed lines.

loss of trochlear and oculomotor foramina. The derivation of the derived state may be viewed as an anterior displacement of the nerve complex, possibly the result of temporal readjustments in the ontogeny of the brain and nerve trunks relative to the osteological development of the cranium (Fig. 12G).

Loss of the pars jugularis giving rise to a common optic-olfactory-trigeminal foramen is considered a synapomorphy for Gadiformes, linking Gadoidei with Macrouroidei (Howes, 1989; 1990; 1991). That a similar large-scale modification should also occur among ophidiiforms in what are apparently separate lineages questions the homologous *versus* homoplastic nature of the macrouroid and gadoid character.

Dorsocranial morphology

Gosline (1953) remarked on the nature of the parietals in ophidiiforms. Of the three taxa he examined, only in one, *Dinematichthys*, do the parietals meet in the midline. Cohen
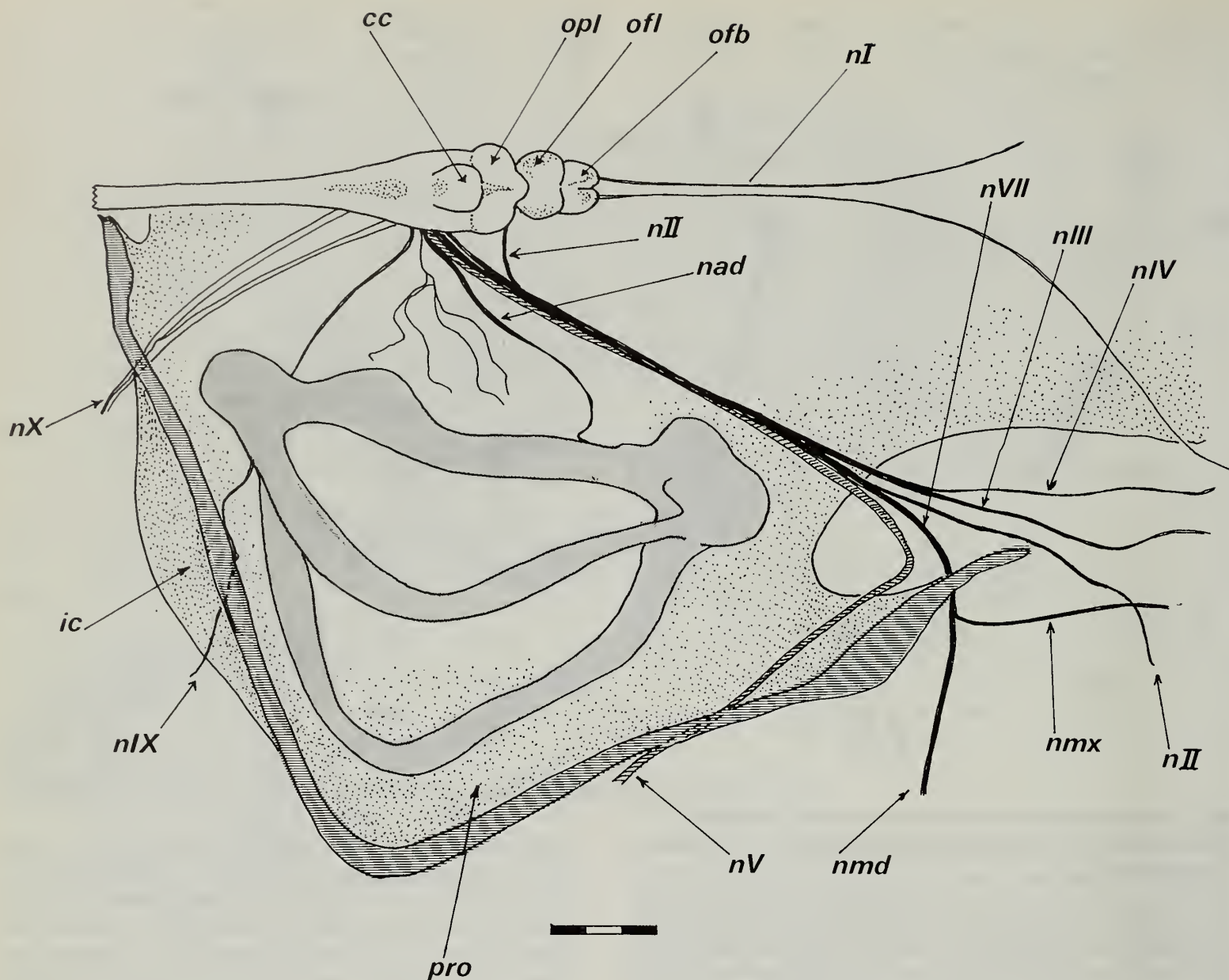
Fig. 11　*Acanthonus armatus*: brain and cranial nerves in dorsal view; the semicircular canals are shown in light shading.

(1974) shows that in *Brotulotaenia* the parietals almost meet anterior to the supraoccipital but are otherwise widely separated. In all the genera I have examined, the parietals are separated by the supraoccipital. In *Brotulotaenia* and in *Enchelybrotula* the parietals are extensive, being half the length of the frontals (Cohen, 1974; 1982) and although there is some variation in size in the genera examined, most do not exceed 25% of the frontal length. In *Acanthonus* the parietals are widely separated by the supraoccipital (the separation almost equals the width of the parietal; Fig. 13A); such wide separation occurs only in *Cataetyx* and *Bathyonus* (Figs 13C & 14A), taxa with broad and depressed crania.

There is considerable variability in frontal morphology among the taxa examined. *Acanthonus* differs from other genera in having the anterior border of the frontal laterally flared. In other taxa the frontal tapers anteriorly. The exception is *Glyptophidium* (Fig. 14E) where the frontal has a broadly rounded anterior margin and a straight lateral border. *Genypterus, Brotula* (Fig. 15B), *Sirembo* and *Spectrunculus* (Fig. 14B) have an extensive laterally open frontal canal. Anterior frontal crests, arising at the point where the bones meet the ethmoid bloc occur in *Lamprogrammus, Monomitopus, Neobythites, Sirembo* and *Glyptophidium*, the latter also having posterior crests at the junction of the frontal and supraoccipital (Fig. 14E). Frontal crests similar to those of *Glyptophidium* also occur in carapid ophidiforms (Fig. 21B of *Onuxodon* in Markle & Olney, 1990). A deep anterior medial cavity in the frontal midline, similar to the 'mucosal cavity' of gadoids occurs in *Monomitopus* and *Lamprogrammus* (Fig. 13B).

The autosphenotic of *Acanthonus* has a long, thick posteriorly curved lateral process (Fig. 13A). Of the taxa examined, only in *Spectrunculus* (Fig. 14B), *Monomitopus* (Fig. 14C) and *Brotula* (Fig. 15A) is the sphenotic process directed posteriorly but in these taxa it is small and spine-like. In other genera the process is either laterally or anteriorly directed. In *Genypterus* the sphenotic extends anteriorly to halfway beneath the length of the frontal (Fig. 15B).

The pterotic of *Acanthonus* has a prominently rounded posterior margin, a condition approached only by *Bathyonus* (Fig. 14A). In other genera examined the pterotic has a blunt or pointed posterior border.

Regan (1929) surmised that direct contact between frontal and parasphenoid diagnosed ophidioids (and blennioids); he had earlier (1912) illustrated this condition in *Brotula* where the frontal meets the anterior part of the parasphenoid
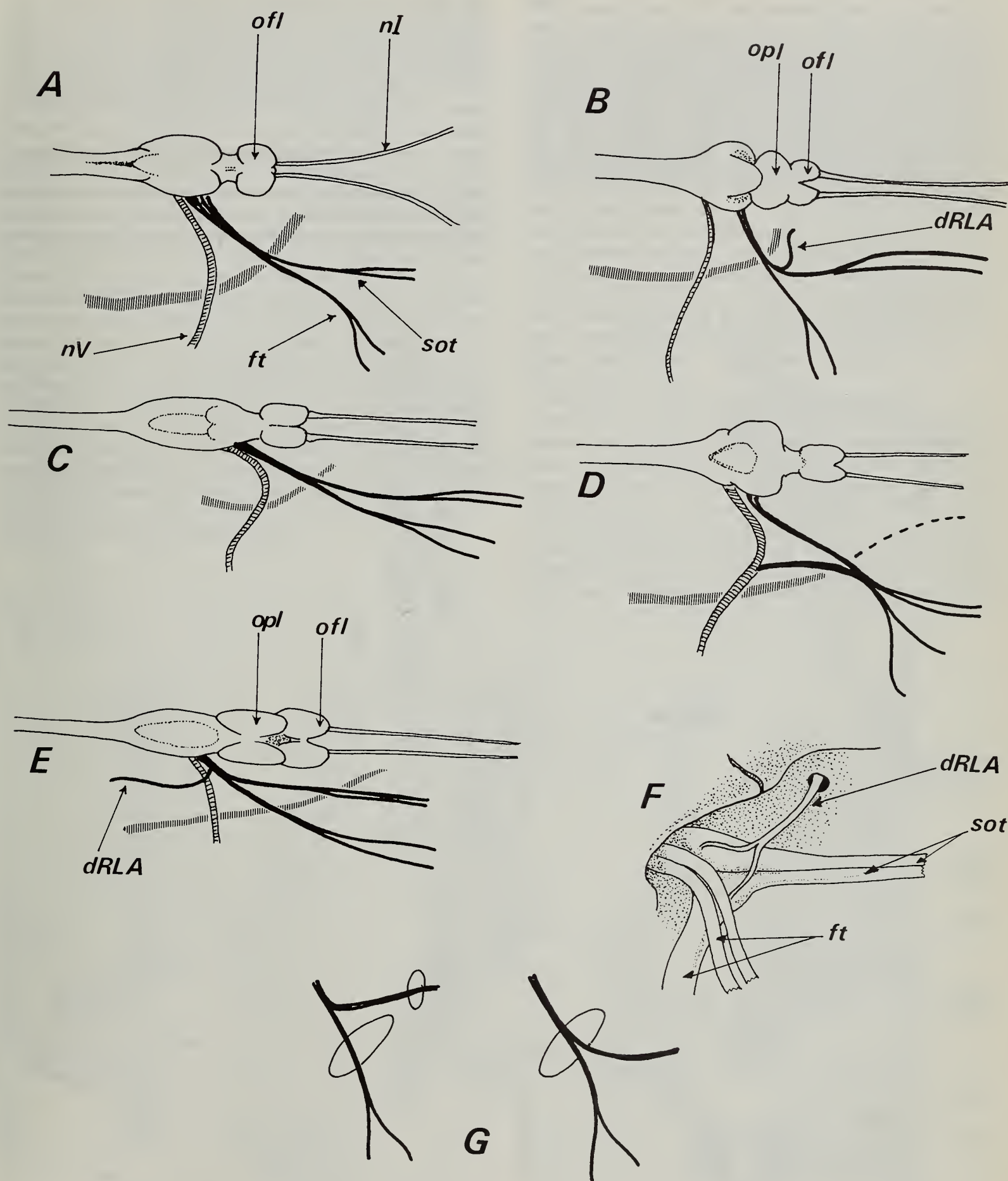
Fig. 12 Cranial nerve courses (semi-diagrammatic) in A, *Neobythites gilli*; B, *Lamprogrammus niger*, C, *Cataetyx* sp., D, *Bassozetus* sp., E, *Genypterus blacodes*, F, *Penopus* sp. Trigeminal branching external to the facialis foramen (ventrolateral view), G, Hypothesised shift of branching point of infraorbital and supraorbital nerves. Left, plesiomorphic ophidiiform condition (circular outlines represent foramina); right, derived condition with exit *via* single foramen and branching external to it. Shaded strips denote cranial wall.

ascending process. Gosline (1953) also recorded the condition in *Brotula* and *Dinematichthys*. Of the taxa I have examined, apart from *Brotula* (Fig. 10C), the feature occurs only in *Sirembo* and is thus certainly not diagnostic for ophidiiforms. However, among the Carapidae the frontal appears to contact the parasphenoid ascending process in nearly all the taxa illustrated by Markle & Olney (1990), the exception being *Encheliophis*. In view of the established monophyly of the Carapidae (Markle & Olney, 1990), the similar condition in the ophidiids (*Brotula*, *Sirembo*) and bythitid (*Dinematichthys*) appears to have arisen independently.

Olfactory nerve tracts

Gosline (1953) noted that the olfactory nerve pathway differed between *Brotula* and *Dinematichthys*. In the former the tracts are enclosed in a canal formed by the frontal and diverge from one another anteriorly, while in the latter, the tracts are free and diverge immediately from the olfactory lobes of the brain. In the taxa examined the variability is similar. In *Acanthonus* the tracts lie parallel for some distance before diverging (Fig. 11); the width of the cranial cavity allows a broad, unimpeded divergence of the tracts which lie medial to the sagittal interorbital membranous septa. This situation obtains in *Bassozetus*, *Lamprogrammus*, *Glyptophidium* and *Genypterus* (Figs 12B, D & E) but in other
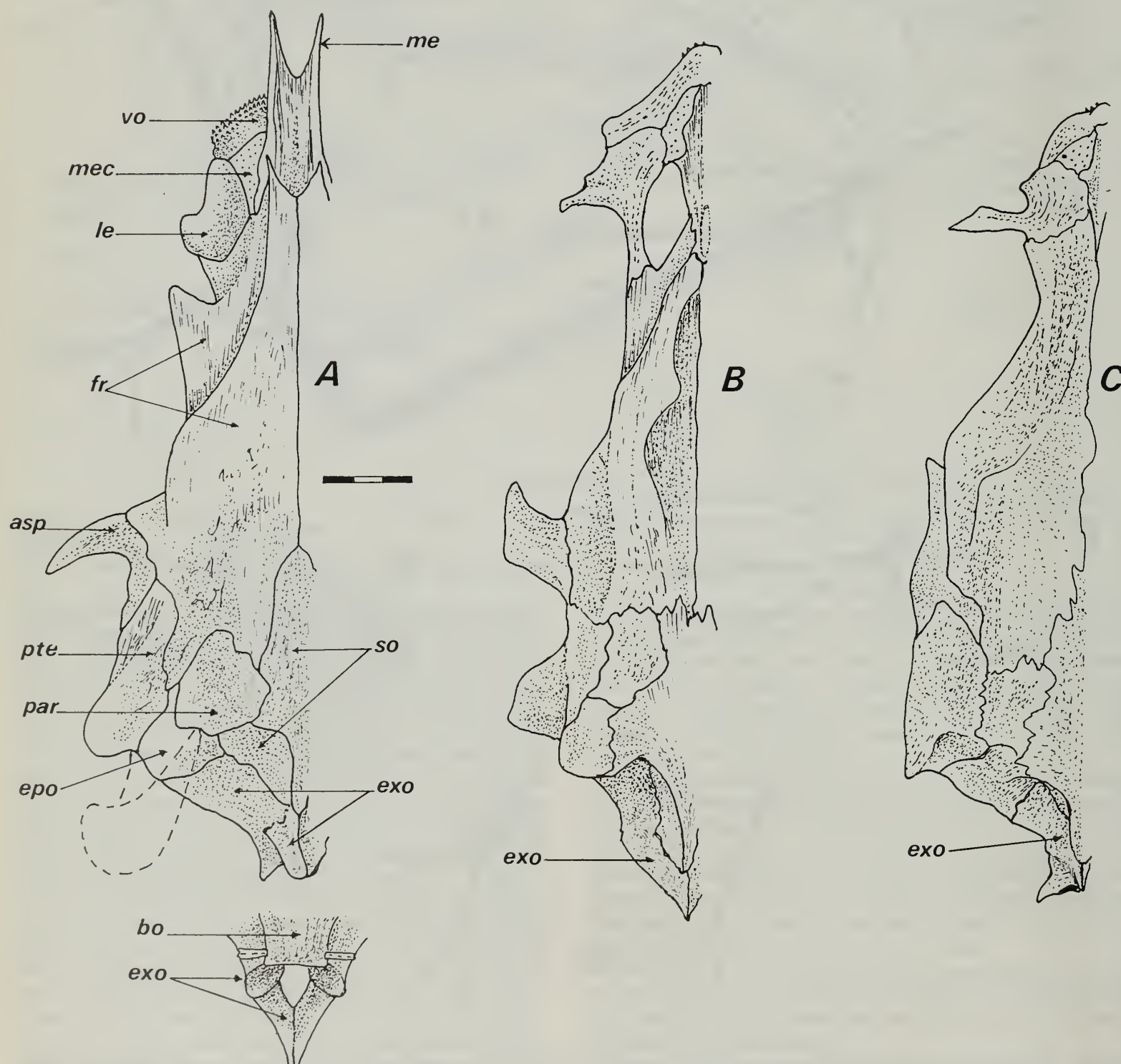

Fig. 13   Crania in dorsal views of A, *Acanthonus armatus*; B, *Lamprogrammus niger*; C, *Cataetyx sp.* In A, the posttemporal is indicated by dashed lines; below is a ventral view of the occipital condyles to show the extension of the exoccipital facets beyond the basioccipital facet.

genera the tracts are broadly divergent. In part these patterns are due to the distance between the forebrain and the olfactory organs which in *Brotula* is short, principally on account of the brain being particularly large and extending well forward. In *Monomitopus* a somewhat different situation occurs in that the forebrain enters the orbital cavity, the tracts running parallel for a short distance then diverging.

Position of glossopharyngeal foramen

Gosline (1953) referred to the varying position of the glossopharyngeal nerve foramen, apparently perforating the exoccipital in *Dinematichthys* and the intercalar in *Brotula*. Patterson & Rosen (1989) report that in all ophidiiforms they examined the foramen occurs in the intercalar. In *Acanthonus* an external examination of the cranium fails to locate the glossopharyngeal foramen. The fretted and honeycombed nature of the bone disguises any small foramina and its papery thinness is easily accidentally pierced giving rise to artificial 'foramina'. By following the route of the glossopharyngeal nerve within the cranial cavity it can be ascertained that the nerve exits from the posterodorsal border of the intercalar above the articulation of the lower limb of the posttemporal (Fig. 8). In other taxa examined for this feature the foramen is usually located in the centre of the intercalar either beneath or, more rarely, posterior to the site of attachment of the posttemporal limb.

Exoccipital, occipital condyles and first neural arch

Rosen & Patterson (1968: 425) noted that one of the features distinguishing gadiforms and ophidioids was the presence in the latter of a '. . . complex basioccipital joint with the first vertebra, involving the formation of a bony arch between the foramen magnum and the basioccipital facet'. Rosen (1985: 29) recognised that the batrachoid-lophiiform and ophidiiform-gadiform groups have the first neural arch and spine ankylosed with the first centrum and joined firmly to the cranium. Rosen (*op. cit.*: 50) in referring to gadiforms and ophidiiforms also noted that in some cases (specific examples were not cited) neural arches are incorporated into the exoccipitals and supraocciptal. Howes & Crimmen (1990) recognised such an incorporation in the neobythitine ophidiiform *Lamprogrammus* in which they identified both an incorporated neural spine and arch which formed the 'exoccipital' condyle and the first centrum which formed the 'basioccipital' condyle.

Although it is evident in all the ophidiiform taxa I have examined that there is a complete arch forming the rear of the cranium and bordering the posterior margin of the supraoccipital it appears that it is the occipital arch and not an incorporated neural arch. Evidence that it is the exoccipital is the presence of a suture with the entire length of the basioccipital and an unbroken suture with the supraoccipital. In many specimens the suture with the basioccipital is almost impossible to discern but the maceration of crania in both KOH and by boiling in water readily reveals the exoccipitals
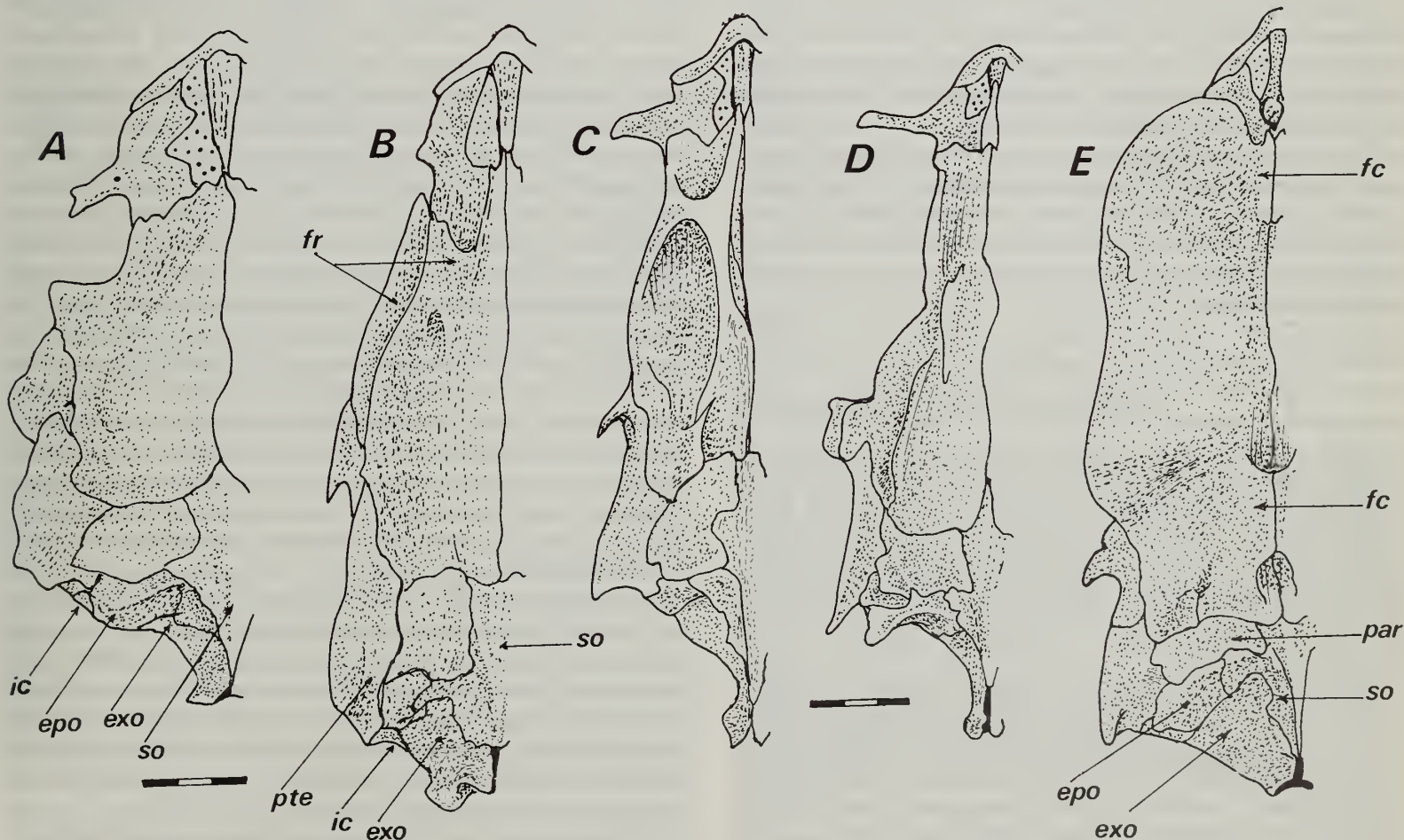

Fig. 14 Crania in dorsal views of A, *Bathyonus* sp.; B, *Spectrunculus grandis*; C, *Monomitopus metriostoma*; D, *Neobythites steatiticus*; E, *Glyptophidium macropus*.
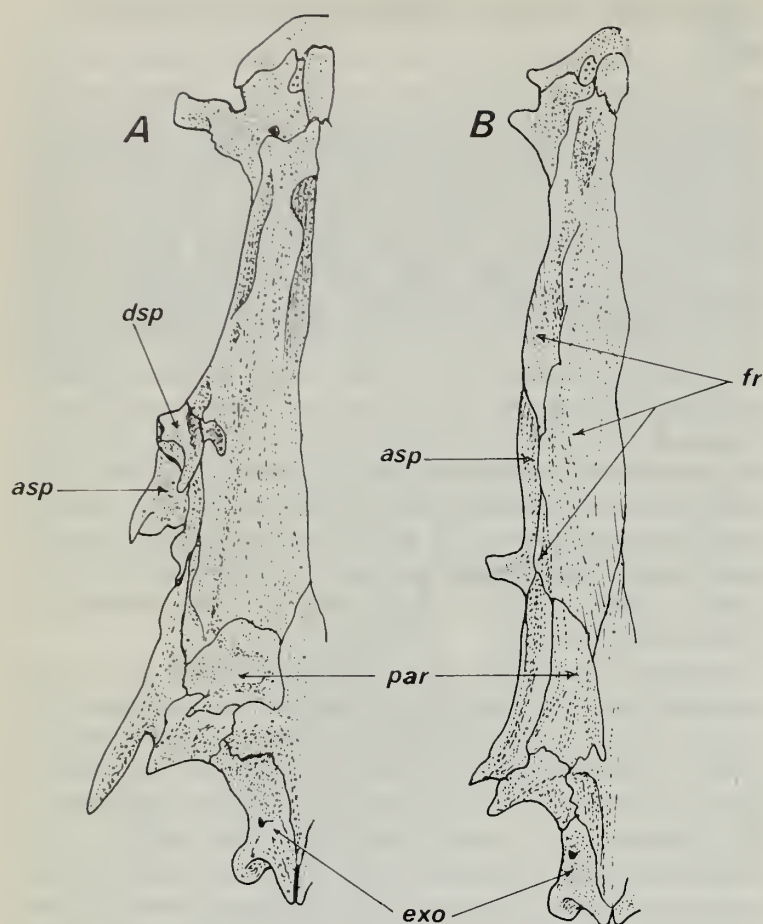
Fig. 15 Crania in dorsal views of A, *Brotula multibarbata*; B, *Genypterus blacodes*.

Fig. 16 Cranial-vertebral articulation in A, *Neobythites steatiticus* and B, *Ophidion rochei* (lateral views).

as single elements. Furthermore, in cleared and stained specimens cartilaginous laminae border the bones along the midline where they meet to form the floor of the foramen magnum. A foramen lying posterior to that of the vagus nerve transmits the occipital nerve trunk.

The posterodorsal extension of the exoccipital with consequent exclusion of the supraoccipital from the posterior cranial margin is a feature unique to ophidiiforms. In the Carapidae although the exoccipital is dorsally extended it does not rise high enough to occlude the posterior tip of the supraoccipital (Fig. 18C).

Rosen (1985: 50) noted that a possible synapomorphy between gadiforms and some ophidiiforms is the position of the exoccipital facets with respect to the basioccipital and the corresponding anterior extension of the prezygapophyses of the first centrum onto the occiput to meet the exoccipitals. Of the taxa examined here only in *Acanthonus* do the exoccipital condyles extend posteriorly beyond the basioccipital facet (Figs 13A, 18A), a feature otherwise peculiar to pediculate paracanthopterygians (cf. Rosen's 1985 fig. 35B and D). In all other taxa the posterior edge of the basioccipital facet lies in the same vertical plane or slightly beyond that of the exoccipital facets.

Rosen (1985) and Patterson & Rosen (1989) recognised two groups of ophidiiforms by their different occipital condyle morphology: Ophidiidae possess a plesiomorphic 'planar' arrangement of the exoccipital facets and Bythitoidei have derived 'cod-like', widely separated, tubular and cartilage-filled condyles. Rosen (1985, Fig. 36) illustrated *Ophidion* and *Ogilbia* as representing respectively the ophidiid and bythitoid conditions (Rosen's drawing of *Ogilbia* is reproduced here as Fig. 17B). Patterson & Rosen (1989)
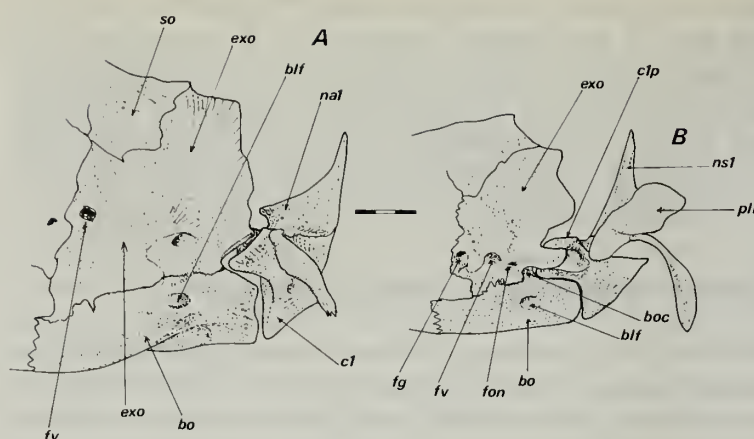
observed the planar condyle feature in *Brotula*, *Genypterus* and *Neobythites* as well as *Ophidion* but they did not list those taxa in which the supposed 'cod-like' articulation occurs. In the taxa examined here I do not find these marked differences (cf. Figs 17 with 16 and 18).

In *Ophidion* (Fig. 19D) the exoccipital facets are medially deep and are united to form a continuous articulatory surface; the lateral part of each facet is extended posteriorly into a 'condyle' and turned ventrad. The basioccipital facet is separated from the exoccipital by a deep forwardly directed cavity (boc). With two exceptions (see below) all other taxa (including the bythitoids *Ogilbia* and *Lucifuga*) have a 'planar' surface formed by medially united exoccipitals (Fig. 19A,B) although not as deep as in *Ophidion*; the lateral, condylar part of the exoccipital (exc) is variously angled and in *Glyptophidium* (Fig. 19F) faces directly ventrad. The basioccipital facet is separated from the exoccipital by a dorsally directed bursa-like cavity (boc) which accepts the ventral facet of the first centrum (c1p, Figs 16B, 19D); see also Rosen & Patterson, 1968, fig. 10D of *Dinematichthys* and Howes & Crimmen, 1990, fig. 27 of *Lamprogrammus*. Apart from *Ophidion* the two exceptions to this condition are *Genypterus* (Fig. 19E) and *Acanthonus* (Fig. 19C), the only two taxa which have medially separated exocciptal facets. In *Genypterus* the separation is marginal but in *Acanthonus* it is extensive, and the facets appear as true 'cod-like' condyles. In *Acanthonus* the exoccipital facets extend beyond the basiocciopital facet (see above) and there is no davity between the basioccipital and overlying exoccipitals. *Genypterus* however, closely resembles *Ophidion* in having a horizontal cavity between the basioccipital and exoccipital facets into which inserts the anteriorly directed medial facet of the first centrum (Fig. 16B).

In ophidiiforms Baudelot's ligament is always confined to the basioccipital and is a consistent marker in separating the dorsal and ventral (which posteriorly become lateral and medial) sections of the epaxial muscle which inserts respectively on the anterior ribs and medial region of the swimbladder (see below). In *Acanthonus* Baudelot's ligament stems not from a fossa on the underside of the basioccipital but from the rim of the facet (Fig. 18A).

The first neural arch and spine display several modifications amongst ophidiiforms. In *Ophidion*, *Brotula* and *Genypterus* the bases of the neural arch are flattened anteriorly and expanded laterally which in *Ophidion* form wing-like
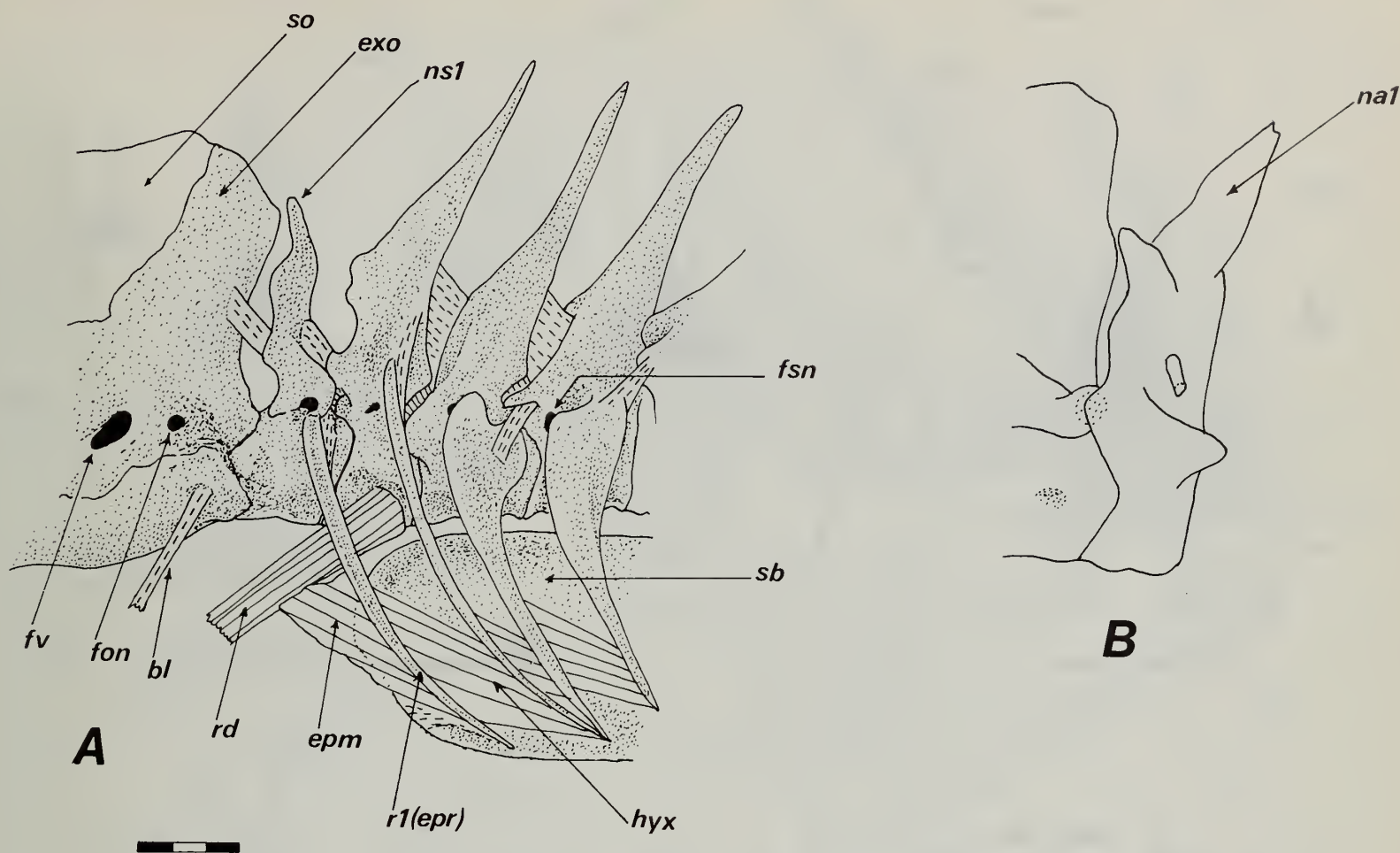
Fig. 17   Cranial-vertebral articulation (left, lateral views) in A, *Ogilbia cayorum*, also showing swimbladder connections (drawn from
dissected and stained specimen); B, copy of Rosen's (1985) figure 36B showing the supposed designation of the first neural arch (guide-line
absent in the original figure) and 'cod-like' condyles.

structures to which attaches a segment of epaxial muscle
(Fig. 16B; Rose, 1961 and below). In some taxa (e.g.
Ogilbia, and *Diplacanthopoma*, only the anterior base of the
arch is autogenous with the centrum (Fig. 17A). In others
including *Acanthonus*, *Bathyonus* and *Penopus*, (Figs 18A;
24B & C) the arch is reduced to a slender bone, the base of
which is supported by only a narrow pedestal on the lateral
ridge of the centrum. In other taxa (*Lucifuga* and *Spectruncu-
lus*, Figs 23A; 25A) the neural spine has been lost, leaving
the base of the neural arch autogenous and attached by post-
and prezygapophyseal ligaments respectively to the succeed-
ing neural arch base and the epioccipital.

It seems that among ophidiiforms and pediculates the skull
has been posteriorly extended, in the former group by the
dorsoposterior expansion of the exoccipital and in the latter
by expansion and ankylosis of the first neural arch. Although
there are similar modifications to the exoccipital-vertebral
contact in pediculates and ophidiiforms the resemblances are
not as close as recognised by Rosen (1985) and Patterson &
Rosen (1989) so as to unite pediculates with bythitoids. As
noted above, in almost all ophidiiforms the exoccipital articu-
latory facets form a continuous medial surface and the lateral
margins retain a condylar form even though the articular
surfaces may be variously shaped and angled. In pediculates,
however, there is no continuous exocciptal facet and the
lateral 'condyles' are so modified as to have lost their
condylar nature and in those taxa where they appear strut-
like, their articular surfaces are sutured with those of the
prezygapophyses of the first vertebra. There is no truly
'cod-like' cranial-vertebral articulation in any ophidiiform

examined here and cartilage cores are present in all their
exoccipitals. The most notable feature of the ophidiiform
articulation is the presence in the majority of taxa of the
angled bursa-like cavity lying between the exoccipitals and
basioccipital and which occurs in all ophidiiforms and cara-
pids (Fig. 18C). Markle & Olney (1990: 277) have drawn
attention to this feature in referring to the medial ventral
facet of the first centrum and it would seem that the modified
basioccipital-vertebral articulation is a synapomorphy for
ophidiiforms (including Carapidae).

Swimbladder and its connections

Acanthonus lacks a swimbladder, in which respect it appears
to be derived (see below). The 28 genera examined for this
feature display a plethora of conditions of swimbladder-
vertebral column association. The variable nature of the
association is revealed in muscle attachments, number and
degree of hypertrophy of anterior ribs, their position on the
vertebral column and features of the swimbladder itself. In
addition the nature of the first free neural arch (discussed
above) appears to be intimately connected with specific types
of swimbladder-vertebral associations.

There are two basic types of swimbladder-vertebral con-
nections:

(1) having the first (enlarged) rib attached to the first centrum
and it and ribs 2 and 3 thickened with ribs 2 and 3 often
expanded, extending horizontally and partially covering the
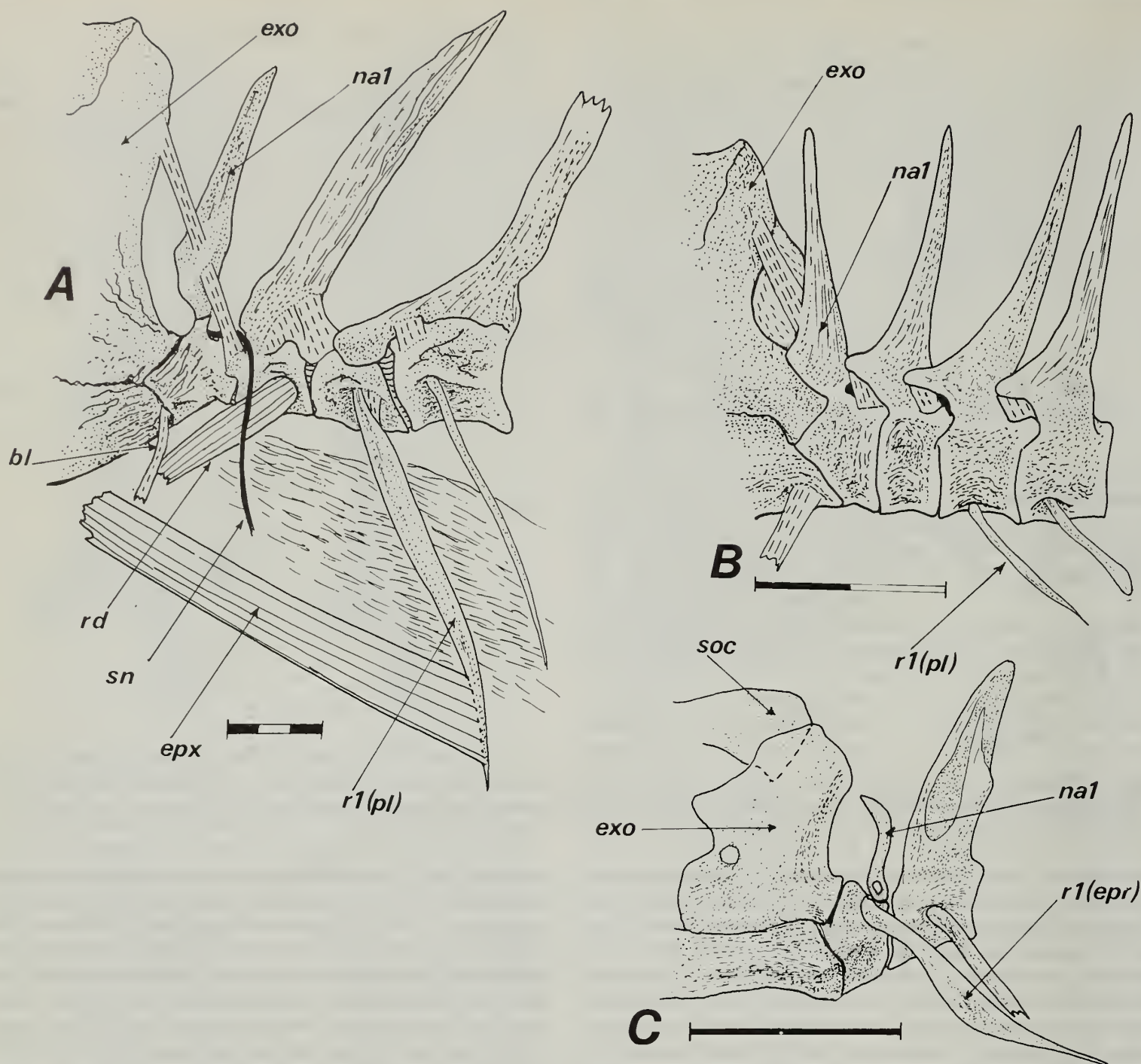anterodorsal surface of the swimbladder; the distal tips of all

Fig. 18 Cranial vertebral articulation in A, *Acanthonus armatus*, also showing associated musculature (left, lateral view); B, *Barathronus bicolor*, membrane (hatched area covers space between exoccipital and first neural arch and spine; right side, lateral view; drawing reversed); C, *Carapus bermudensis*, (left, lateral view of cleared and stained specimen).

three ribs are attached to the swimbladder wall and well-developed muscles (lateral and medial) run between the cranium and first rib-swimbladder wall. The swimbladder is situated well forward, its anterior wall thickened by sclerification or ossification and sometimes the outer wall forms a flap or 'door' or separate elements (rocker bones) which are ligamentously attached to the ribs. A subgroup of taxa can be distinguished in which the first rib, although thickened is never expanded.

(2) having the first (large) rib attached to the second or third centrum, it and ribs 2 and 3 normal, vertical or somewhat posteriorly directed, all are free from the swimbladder. A narrow, outer band of epaxial muscle connects the first rib to the basicranium and a medial band runs to the dorsoanterior wall of the swimbladder. The swimbladder is situated far back, between the fifth and eighth centra and its anterior wall lacks any sclerification or thickening.

Some of the variation within these groupings is detailed below.

Group 1. Examined taxa with these features are Brotula, Cherublemma, Genypterus, Hypopleuron, Lepophidium, Ophidion, Parophidion

Rose (1961), Svetovidov (1961) and Courtenay (1971) have made detailed descriptions of the swimbladder and its cranial-vertebral connections in *Ophidion* (given as *Rissola* by Courtenay). These authors showed that sexual dimorphism is exhibited in the morphology of the swimbladder connections, the principal differences being the presence of an anteroventral element in males termed the 'rocker bone' by Rose (1961). The anterior pair of ribs are extended into wing-like structures which support the edges of the rocker bone (Fig. 16B). The expanded third rib forms a bony sheet
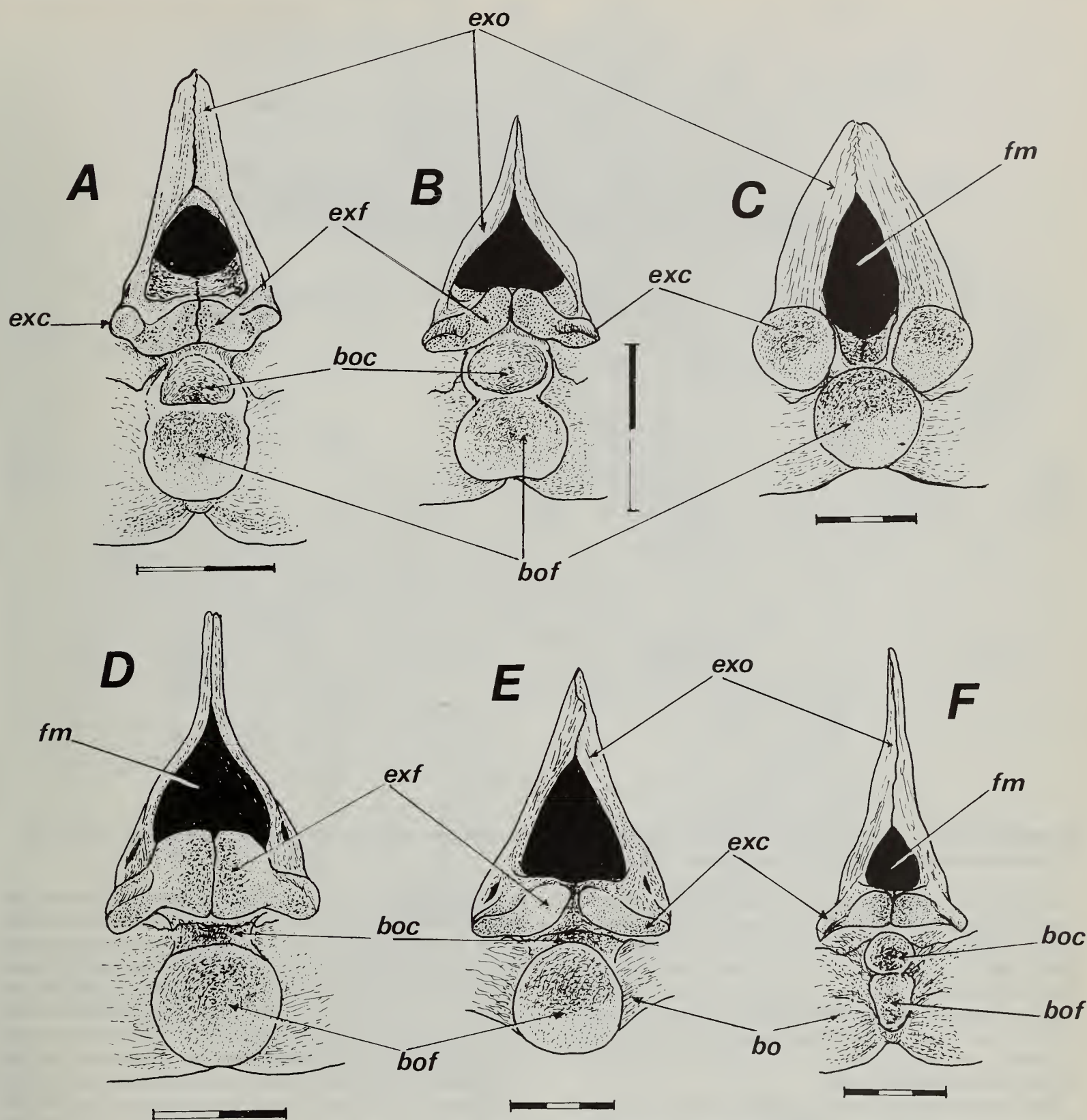
Fig. 19 Posterior views of occipital condyles of A, *Neobythites steatiticus*; B, *Ogilbia cayorum*; C, *Acanthonus armatus*; D, *Ophidion rochei*; E, *Genypterus blacodes*; F, *Glyptophidium macropus*.

covering the anterior region of the swimbladder. In these taxa the first neural arch is also modified (see above). Apart from *Ophidion*, *Brotula* is the only other examined genus to possess a rocker bone.

In *Cherublemma* (Fig. 20) the third and fourth-sixth ribs (possibly a combination of vertebral parapophysis and rib) are enlarged to form an ossified shield over the anterior part of the swimbladder; the anterior wall of the swimbladder (tunica externa) is almost completely excised, being attached by a ventral hinge and forming a 'trap-door' (sbc, Fig. 20) which is attached

on either side of its upper rim to the tip of the first rib by a ligament (lcc, Fig. 20). When opened the door exposes a fenestra covered by the tunica interna (ti, Fig. 19B). The ribs of the third vertebra join together in the ventral midline to form a broad bony surface with paired depressions on which the dorsal lip of the 'door' closes. *Hyplopleuron* (Fig. 21) also has the first-third ribs expanded to the same degree; the tunica externa of the swimbladder is dorsally sclerified and laterally and ventrally the swimbladder is sequentially constricted, resembling the body of a caterpillar.
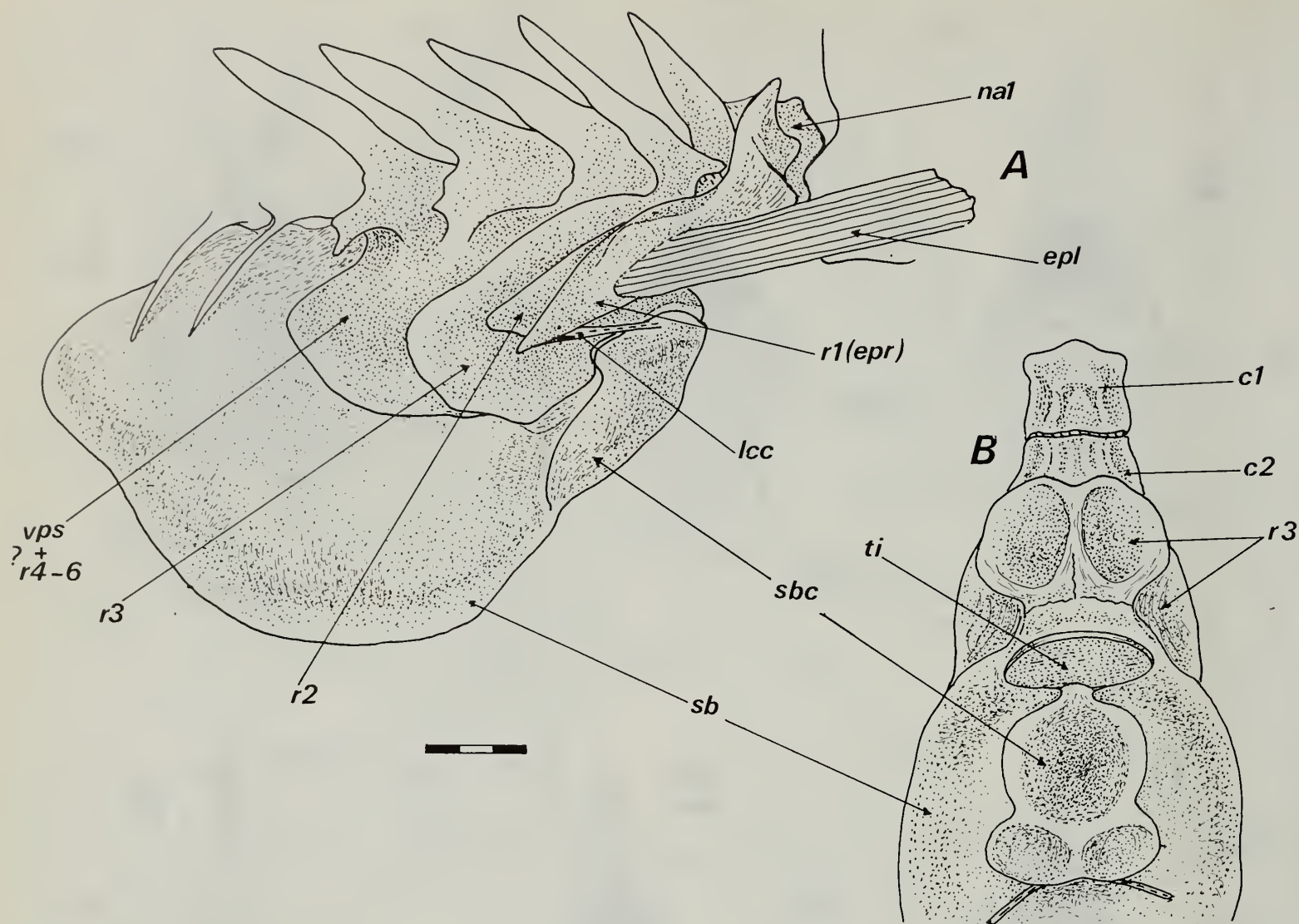
Fig. 20 *Cherublemma emmelas* (female). Anterior vertebral column and swimbladder in A, right lateral and B, ventral views. In B the cap of the swimbladder is shown reflected and with the ligaments cut away.

Owing to its expanded first rib and neural spine, *Lepophid-ium* (Fig. 22A) is also included in this group but there are several differences between it and the other included taxa. Ribs 2 and 3 are slender and rib 1 is attached to the head of the swimbladder by a thick, semi-ossified ligament which runs from the distal tip of the rib to bifurcate behind the second rib, the two branches (of normal ligamentous consistency) attaching to respective sites on the anterolateral and dorsal areas of the swimbladder wall.

Taxa recognised as forming a subgroup (see above) are: *Brosmophyciops, Dicrolene, Glyptophidium, Lamprogram-mus, Monomitopus, Neobythites, Ogilbia, Pycnocraspedium, Petrotyx, Sirembo.*

In these genera the first–third ribs are stout but the first, unlike that of other Group 1 taxa, is not produced into a wing-like structure but resembles them in having the distal tips of the ribs ligamentously united and attached to the wall of the swimbladder (Fig. 22B). A separate muscle attaching to the medial part of the swimbladder occurs in some taxa (in *Brosmophyciops* it is particularly well-developed); the lateral band runs from the epi- and exoccipital regions of the cranium to join the compound swimbladder-rib ligament.

Lamprogrammus (Fig. 21) has a distinctly modified swim-bladder and attachment. The expanded first–third ribs are entirely enclosed in silvery connective tissue which appears to

be an extension of the compound ligament that invests the distal tips of the ribs in other Group 1 taxa; the nature of the tissue suggests that it might even incorporate the tunica externa of the swimbladder. The swimbladder itself is finger-like with a bulbous anterior cap, partially detached and hinged on its underside to the body of the bladder (sbc). When closed the dorsal rim of the cap is covered by a strong lip extending from the dorsal midline of the body of the swimbladder. A segment of the compound ligament attaches to either side of the cap. A paired muscle (epm, Fig. 21B,D) runs from the basicranium to insert directly on the swimblad-der cap either side of the midline. The outer section of muscle (epl, Fig. 21B) runs to the proximal part of the first rib. A thick median ligament (lsv, Fig. 21B,C) stretches from between the ventrally directed parapophyses of the fifth centrum to the anterior lip of the swimbladder. The interior of the swimbladder is packed with dense, almost fibrous material.

In *Glyptophidium* the anterior ribs have a similar associa-tion with the swimbladder as in *Lamprogrammus* except that the swimbladder is more extensive and the tunica externa is firmly united to the underside of the centra by thick connec-tive tissue. The swimbladder has a well-developed sclerified lip and is large and heart-shaped with a ventral opening exposing the tunica interna.
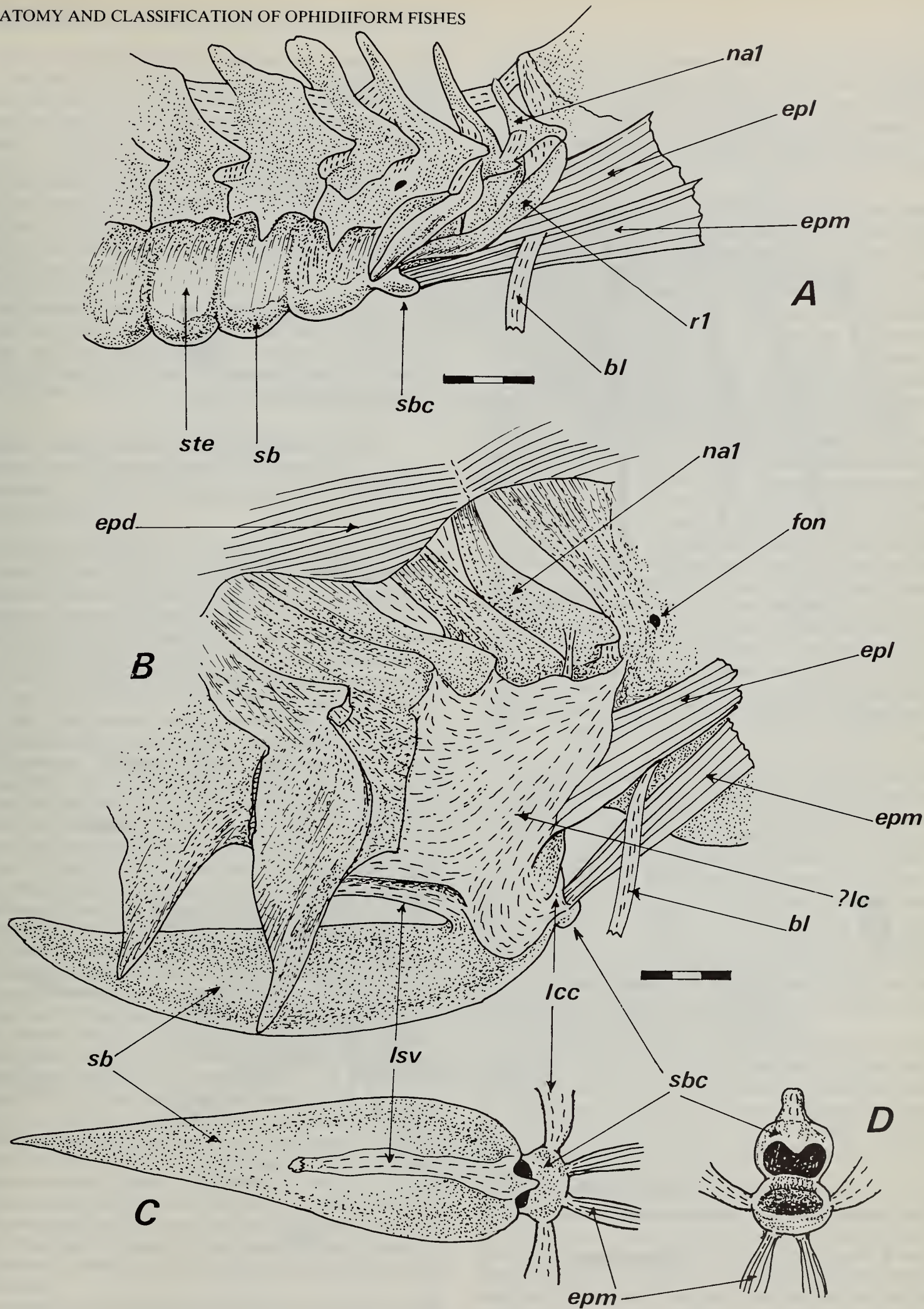
Fig. 21 Swimbladder and its vertebral attachments in A, *Hypopleuron caninum* (male), right lateral view; B–D, *Lamprogrammus niger* (male), in B, right lateral view; C and D, dorsal and anterior views of swimbladder. In A, the ribs are shown as they appear upon superficial dissection, enswathed in ligamentous tissue; in D, the cap of the swimbladder is shown reflected.
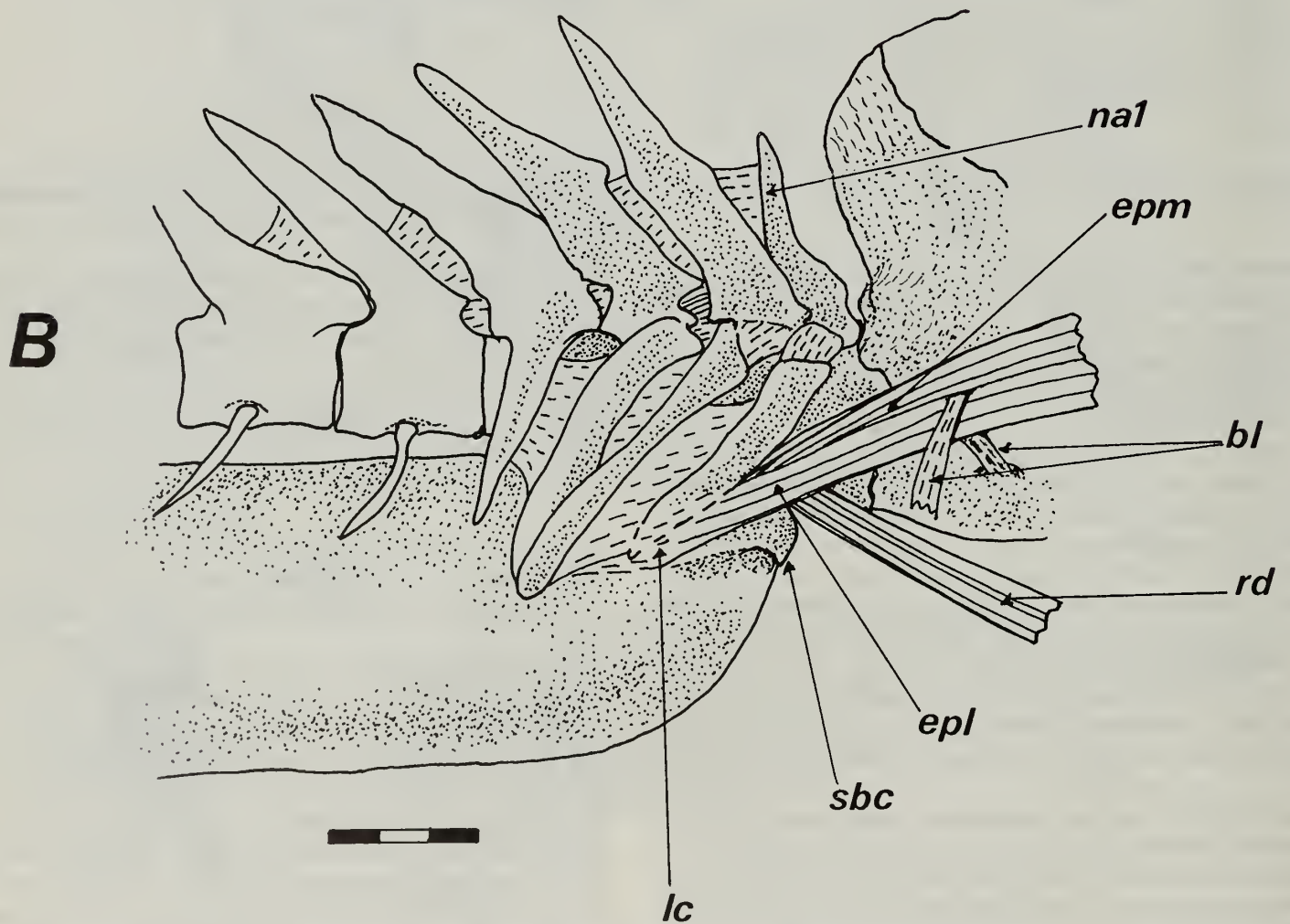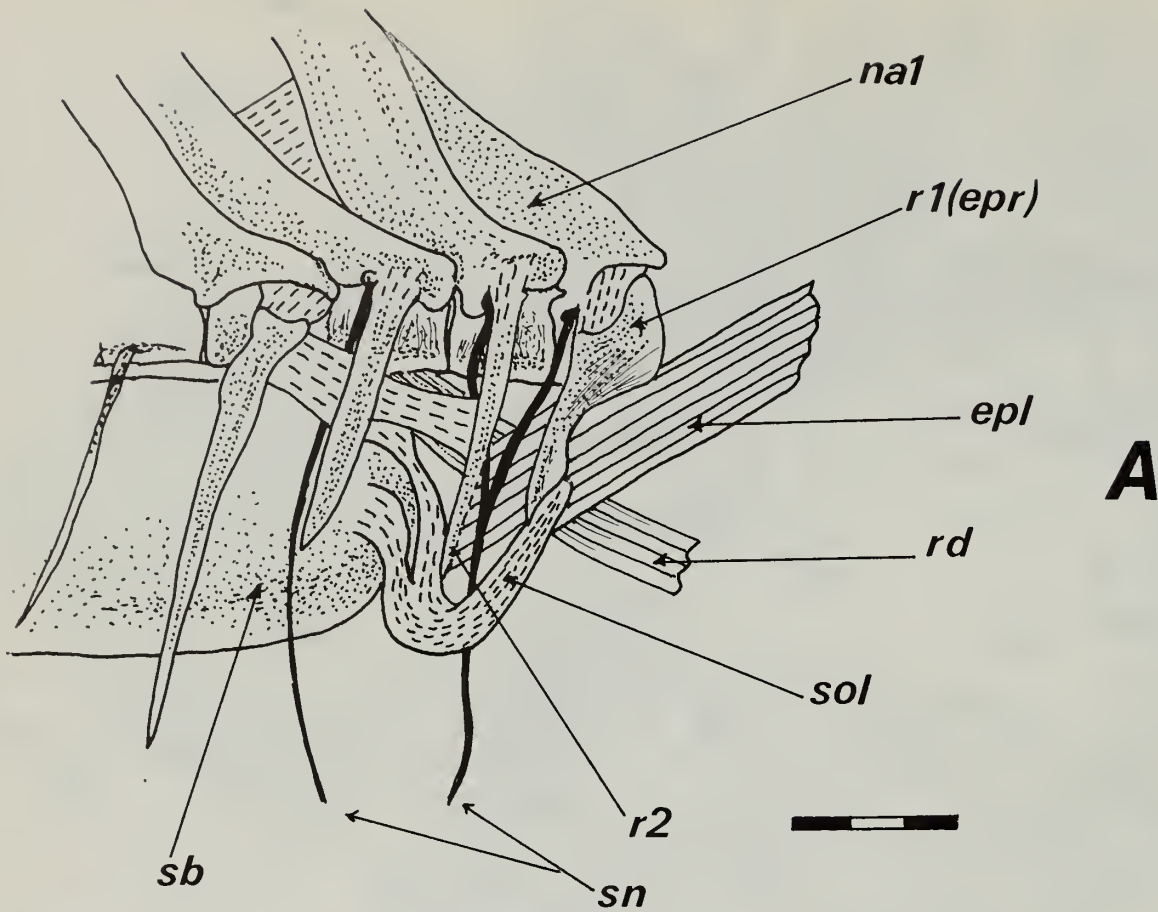
Fig. 22   Swimbladder and its vertebral attachments in A, *Lepophidium cf. profundorum* (female); B, *Monomitopus metriostoma* (female), right lateral views.

Petrotyx and *Ogilbia* stand somewhat apart from the other taxa assigned to this group in having the swimbladder less directly connected to the anterior three ribs (Figs 17A, 22C). In *Ogilbia* (Fig. 17A) the first rib is scarcely thicker than the second although the third and fourth are proximally expanded. In *Petrotyx* (Fig. 23) all three anterior ribs have some expansion, the second only along its proximal part, and both the lateral and medial bands of epaxial muscle insert on the first rib although upper fibres of the medial band also insert on the second rib. The upper part of the outer (dorsal) muscle band passes over the first rib to become continuous with the lateral body epaxial muscle.

Luciobrotula possibly also belongs with this group. The second and third ribs are expanded and joined with the first to the all of the swimbladder by a compound ligament to which a lateral epaxial muscle attaches; there is no medial swimbladder muscle in the specimen examined (a female).

Group 2. Examined taxa with these features are: *Abyssobrotula, Barathrodemus, Bathyonus, Bassozetus, Cataetyx, Diplacanthopoma, Penopus, Spectrunculus*

Taxa of this group exhibit a broad spectrum of conditions but are united on the basis of lacking any great enlargement of the anterior three ribs and in having the first (longest) rib attached to the second or third centrum. The swimbladder is usually located in a posterior position and its anterior rim lies below the fifth-eighth vertebrae; it is elongate and extends to the 20–24th vertebrae. The muscles linking the swimbladder with the cranium have variable morphology; in *Penopus* (Fig. 24A) the muscle has its cranial attachment to the intercalar, pterotic and exoccipital and is divided by Baudelot's ligament, the outer segment attaching to the distal portion of the first rib, the medial segment extending caudad to insert on the dorsal surface of the swimbladder. The tips of the ribs are interlinked with hypaxial muscle but remain free of any direct connection with the swimbladder; in *Bathyonus* the tip of the 1st rib is attached to the postcleithrum (Fig. 24B). *Bathyonus* and *Bassozetus* have a similar arrangement except that in the former the medial muscle is attached to the swimbladder by a long thin tendon (Fig. 24B).

In female *Spectrunculus* (Fig. 25A) the medial segment of the muscle (it passes ventral to Baudelot's ligament) attaches not to the swimbladder but to the peritoneum to which the anterior wall of the swimbladder is itself connected. A pair of large, medial ventral projections, joined in the midline, extend from the fifth centrum in front of which the *retractores dorsales* take their origin. In the male (Fig. 25B) these medially united vertebral processes extend posteriorly in the form of a long deep strut to beneath the eighth or ninth centrum and the lateral epaxial muscle band inserts along the face of the strut. Separate, paired muscles run horizontally from the posterior border of the united vertebral processes above the strut inserting on either side of the dorsal midline of the swimbladder. This muscle is assumed to be a 'detached' part of that medial segment of the *epaxialis* which inserts on the vertebral ventral strut in the male and the peritoneum in the female.

In *Cataetyx* and *Diplacanthopoma* (Fig. 26) there is no separate medial muscle linking the swimbladder (both males and females examined), instead the lateral segment of the epaxial muscle inserts on a compound ligament with the distal tip of the first rib and the swimbladder wall. This situation is similar to that in taxa of the subgroup in Group 1 but differs in that the first rib of *Diplacanthopoma* and *Cataetyx* is curved anteriorly and a band of epaxial muscle distinct from the lateral myomeres runs diagonally backwards from the point of attachment of the first rib to the fourth or fifth rib (eps).

My observations on a single specimen of *Barathrodemus* sp. indicate that it belongs within this group of taxa but they also conflict somewhat with those of Carter & Musick (1985) on many specimens of *B. manatinus*. I do not find a separate pair of muscles connecting the fourth pair of ribs with the prootic; the only muscles in this position are the *retractores dorsales* which extend from the fourth centrum to the pharyngobranchials. Furthermore, in my specimen (a male) the medial muscles connecting the cranium with the swimbladder are separated from the lateral bundle by Baudelot's ligament (the usual condition; see above) and appear to stem from the exoccipital rather than the prootic. The muscles are tendinously joined to the anterodorsal surface of the swimbladder which lies below the eighth or ninth centrum and not the third as indicated in Carter & Musick's specimens. In most respects *Barathrodemus* most closely resembles *Penopus*. Although *Acanthonus* has no swimbladder, features of the vertebral column such as the slender anterior ribs, the first rib articulating with the third centrum and the first neural arch reduced and basally supported on a narrow pedestal (Fig. 18A) indicate its inclusion in this group. That *Acanthonus* has secondarily lost a swimbladder is suggested by the insertion of the lower (medial) segment of epaxial muscle to the first rib, rather than the upper (lateral) segment. Since it is the medial segment which inserts on the swimbladder, indications are that this segment has 'replaced' the original lateral connection.

Lucifuga (Fig. 23A,B) resembles taxa of Group 2 in having unexpanded ribs, however, the first rib associated with the swimbladder articulates with the base of the first centrum and the swimbladder is situated anteriorly as in Group 1 (Fig. 23A). The lateral muscle band attaches to the distal tip of the first rib and the swimbladder wall and there is no medial swimbladder muscle (in the male specimen examined), all features of the subgroup of Group 1 taxa. The lateral muscle band is, however, undivided by Baudelot's ligament which suggests that the lower and medial part of the muscle normally inserting on the swimbladder has been lost. Furthermore, Baudelot's ligament passes between two branches of the vagus nerve (Fig. 23A).

In the only aphyonid examined for these features, *Barathronus* (Fig. 18B), there is no swimbladder, the first pair of ribs articulating with the third centrum but having no muscular connections. According to Nielsen (1969) aphyonids lack ribs but the articulation with the ventral cavity of the 3rd centrum indicates that these processes are pleural ribs (see below).

Markle (1989) states that ophidiiforms typically have epipleural ribs on at least the first two centra and pleural ribs on all succeeding centra, citing *Porogadus* as exceptional in lacking epipleurals from the first two centra (Carter & Sulak, 1984). However, one group of ophidiiform, classified above as Group 2, consistently lack ribs from the first and often the second centrum and when ribs do occur they are short (e.g. *Spectrunculus*, Fig. 25A).

Markle (1989), Markle & Olney (1990) and Patterson & Rosen (1989) consider the anterior ribs to be epipleurals, a
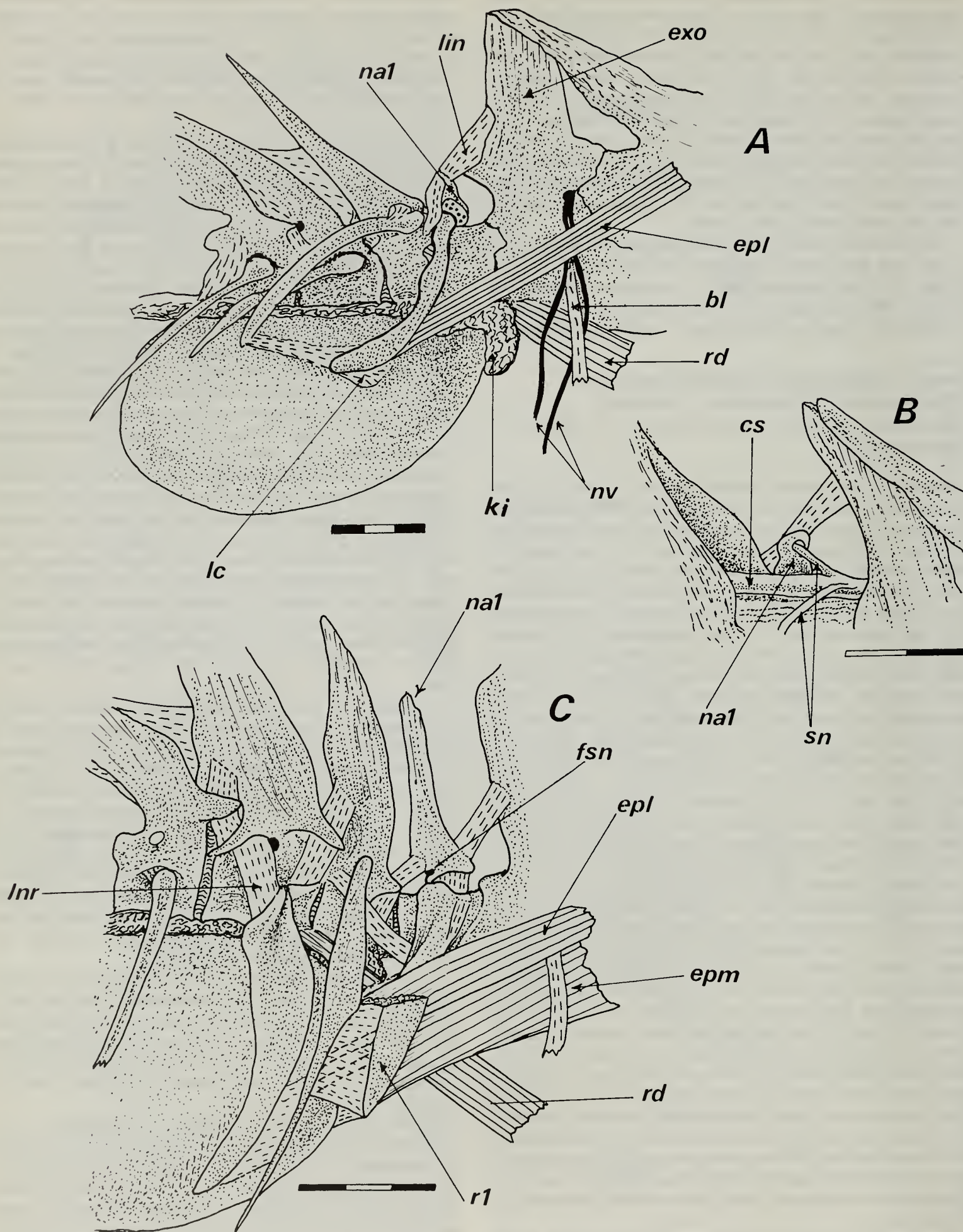
Fig. 23 Swimbladder and its vertebral attachments in A, *Lucifuga dentata* (male), right lateral view; B, dorsolateral view of the first neural arch; the near-side has been removed to expose medial aspect of opposite half of the arch and the central spinal nerve and its associated branch; C, *Petrotyx sanguineus* (sex not determined), right lateral view.
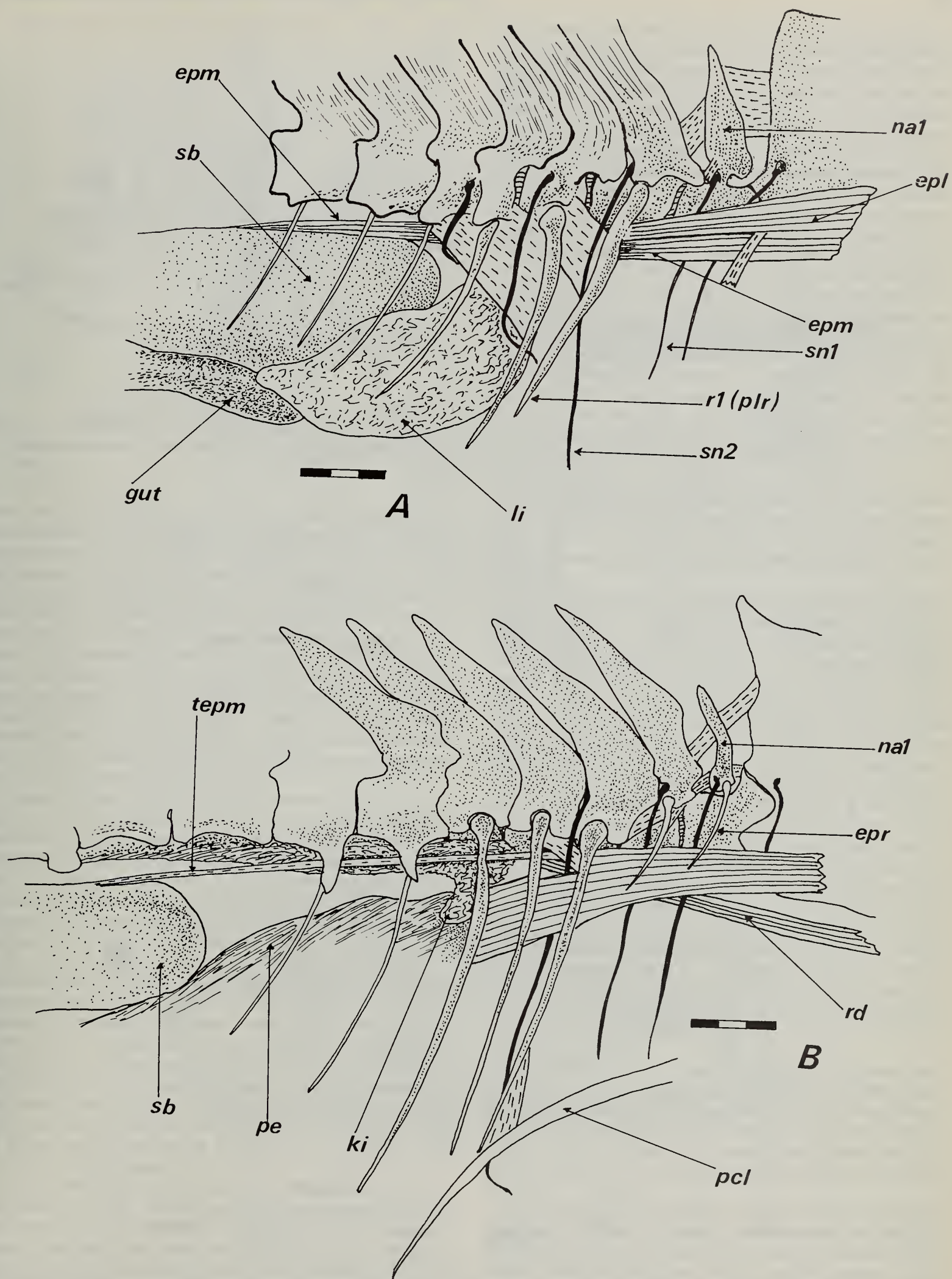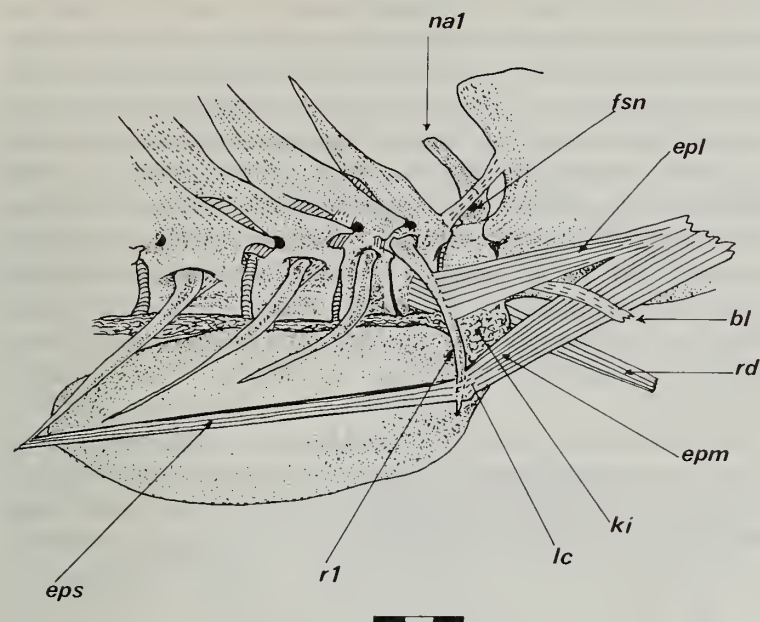
Fig. 24 Swimbladder and its vertebral attachments in A, *Penopus* sp. (male); B, *Bathyonus* sp. (female), right lateral views.

Fig. 25   Swimbladder and vertebral attachments in *Spectrunculus grandis*. A, female; B, male, dashed line indicates margins of vertebral process, right side lateral views.

Fig. 26 Swimbladder and vertebral attachments in *Diplacanthopoma brachysoma* (sex not determined), right side lateral view.

view based principally on their topographical arrangement (see caption to fig. 8 in Patterson & Rosen, 1989). I would suggest that a further indication of their identity is given by the nature of their articulation, namely to the base of the neural spine (in *Ogilbia cayorum* the first epipleural articulates directly with the stem of the neural spine, Fig. 17A). In taxa of Group 2 all the ribs, apart from those on the anterior centra of *Spectrunculus* and *Bathyonus*, are pleural, that is they articulate with the ventral cavity of their respective centrum (Rosen, 1985: 50), none are expanded or directly associated with the swimbladder. Carter & Musick (1985) identify both a stout pleural and an epipleural rib associated with the first centrum in female *Barathrodemus* whereas in the male only an epipleural is present.

Markle & Olney (1990) state that ligaments connecting the epipleural ribs are absent in *Brotula* but present in the other ophidiids they examined; they also identify a compound swimbladder ligament uniting the tips of the anterior epipleurals as a synapomorphy for Carapini. I find interconnecting epipleural ligaments in all ophidiiforms examined, including *Brotula*, and a compound swimbladder ligament in those taxa assigned to the subgroup of Group 1.

To summarise the essential features of the swimbladder-vertebral column association: two assemblages of taxa can be recognised on the relationship of the swimbladder with the anterior (epipleural) ribs: those which have direct contact between the swimbladder and the thickened and expanded ribs (Group 1 above) and those where the swimbladder is isolated from the ribs which are nearly all pleural and never expanded (Group 2 above). Both assemblages contain taxa in which muscles connect the swimbladder with the cranium and in which sexual dimorphism is apparent in the presence/absence of medial muscles.

In the assemblage with expanded epipleurals there are modifications to the anterior wall of the swimbladder taking the form of sclerification and ossification (rocker bone and hinged openings). The same two assemblages can be recognised on the basis of the first neural arch morphology. In that assemblage with expanded ribs and modified swimbladder it is autogenous, usually thick and posteriorly inclined, whereas

in the other assemblage the arch is usually separated into its two halves which are reduced in size joined ligamentously across the midline and connected to the centrum by a narrow bony or cartilaginous pedestal. It is assumed, based on the condition in other paracanthopterygians, that the expansion of epipleural ribs and their intimate contact with the swimbladder is a synapomorphy as are the various modifications to the anterior wall of the swimbladder. Similar features of the anterior vertebrae and swimbladder, including the development of a rocker bone, also occur in Carapidae (Courtenay & McKittrick, 1970; Markle & Olney, 1990). Markle *et al.* (1983) suggested that the paired sclerified structures of the swimbladder to which the anterior pleural ribs attach (Rose, 1961) may represent the precursor of the rocker bone. The presence of a semi-ossified ligament in *Lepophidium* (see above) which connects the swimbladder to the first epipleural rib suggests that such a structure could be implicated in the evolution of the bone. Markle & Olney (1990) dismiss the rocker bone and sclerification of the swimbladder in carapids as being synapomorphic with other ophidiiforms on the grounds that carapid monophyly is attested by a suite of six other synapomorphies, none of which occur in members of the wider group.

The modification of the first neural arch in both assemblages (expansion and thickening in one and reduction in the other) are seen as alternative derived states from the plesiomorphic slender, caudally sloped condition (Markle & Olney, 1990: 278).

Paired muscles having their connections with the swimbladder are common to both assemblages although a complex, medial division is absent from one subgroup (in Group 1 above) and some taxa of Group 2. The muscles identified here as lateral (dorsal) epaxial (epl) correspond to Rose's (1961) muscle M2 + M3 and Courtenay's (1971) 'dorsal sound producing muscle' and the medial (ventral) epaxial (epm) to Rose's (1961) muscle M1 (which in *Ophidion* and *Brotula* connects the rocker bone to the prootic) and Courtenay's (1971) 'ventral sound producing muscle'. Similar muscles in the Carapidae are named by Courtenay & McKittrick (1970) as respectively the secondary and primary sound producing muscles. The lateral (dorsal) band appears to be a segment of that part of the anterior epaxial muscle which has its attachment primitively to the posterior cranial roof and inserts on the first neural arch (see fig. 5 in Courtenay, 1971); the medial (ventral) segment likewise appears to be that part of the epaxialis which is primitively divided from the lateral part by Baudelot's ligament (see above), interconnects the ribs and its innervated by one of the occipital nerves. The presence of homologous muscles in Carapidae suggest they are primitive for Ophidiiformes *sensu* Cohen & Nielsen (1978).

The *retractores dorsales* muscles commonly originate from the third centrum in most ophidiiforms and Carapidae (Markle & Olney, 1990) but in taxa of one of the two assemblages recognised above as Group 2, the muscle originates from the fourth or fifth centrum (in *Spectrunculus* it runs from the anterior border of the united ventral vertebral processes, Fig. 25).

It is beyond the scope of this paper to attempt ascribing functional attributes to the various swimbladder arrangements described here. Suffice it to say that the swimbladder, anterior ribs and first free neural arch all appear to be elements of a single functional unit. Modifications to the first neural arch may have been signaled by the 'release' of the

constraints imposed by the *epaxialis* due to its reorientation to the anterior ribs. The absence of a swimbladder is, judging by its widespread presence among ophidiiforms, a secondary loss which appears to have occurred independently in *Acanthonus, Typhlonus* and aphyonids.

It is noted that the two morphological groups recognised above correspond with ecological groupings. Group 1 are taxa which all inhabit shallow to mid-depths while Group 2 are taxa which are all deep to abyssal.

Cranial muscles

There are three features in which *Acanthonus* differs from other ophidiiforms: (1) almost the entire lateral face of the *levator arcus palatini* (LAP) is exposed, (2) muscle A1b is reduced to a narrow band originating lateral to LAP, (3) the *dilatator operculi* (do, Fig. 27) is extensive and exposed dorsally.

In all other taxa examined much of LAP is laterally covered by the adductor muscle (Ala and A2) but in *Acanthonus* only the lower border of the *levator* is covered by the adductor (Fig. 27). LAP is posteriorly divided and the hyomandibularis nerve runs through this division before bifurcating into mandibular and hyoid branches medial to the adductor; a separate, thin external branch of the mandibularis breaks through the muscle to innervate the tissue of the posterior part of the dentary. In other taxa the mandibularis externus is well-developed. Among the taxa examined, the size of *Acanthonus* LAP is equalled by *Xyelacyba* and *Tauredophidium* and exceeded only by that of *Spectrunculus* (Fig. 28).

In *Acanthonus* muscle A1b is shallow and thin, originating from the anterior border of the hyomandibular and overlapping the anteroventral tip of LAP. In other examined taxa muscle A1b is usually deep and thick, having a bifurcate
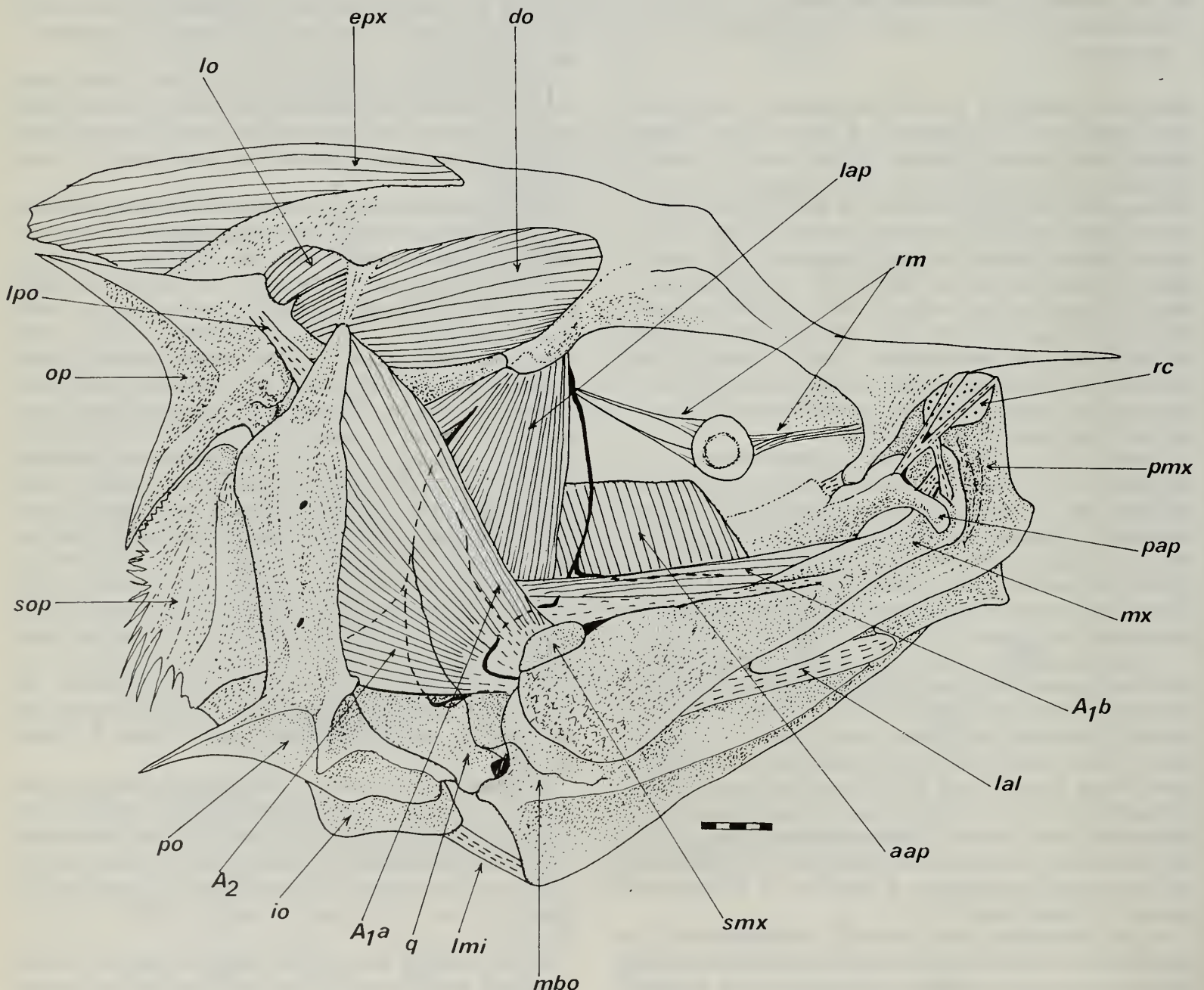

Fig. 27   *Acanthonus armatus*, right lateral view of head showing musculature; the operculum has been elevated to expose the suboperculum and so obscures the *adductor operculi* muscle. Nerves passing medial to muscles are indicated by dashed lines.

origin from either side of the LAP (Fig. 28). The medial segment stems from the metapterygoid or even the ectopterygoid and in *Bassozetus, Dicrolene* and *Spectrunculus* (Fig. 28B) joins the ventral edge of the *adductor arcus palatini*; in *Genypterus* some fibres of A1b even run from the palatine. The lateral portion always originates from the hyomandibular, which in some taxa (e.g. *Bassozetus, Lamprogrammus*; Howes, 1988, Fig. 25) may be the posterior border of the bone.

Muscle A1a was defined by Howes (1988) as that lying lateral to the ramus mandibularis of the trigeminal nerve even though that element might insert on the lower rather than the upper jaw (a more usual definition of A1a is that it inserts on the upper jaw). In ophidiiforms, Howes (1988) reported that the ramus mandibularis passes through the outer muscle bloc and so that section of the muscle lying lateral to the nerve is, by definition, A1a whereas that lying medial to it is A2; *Acanthonus* is no exception to this situation and the major
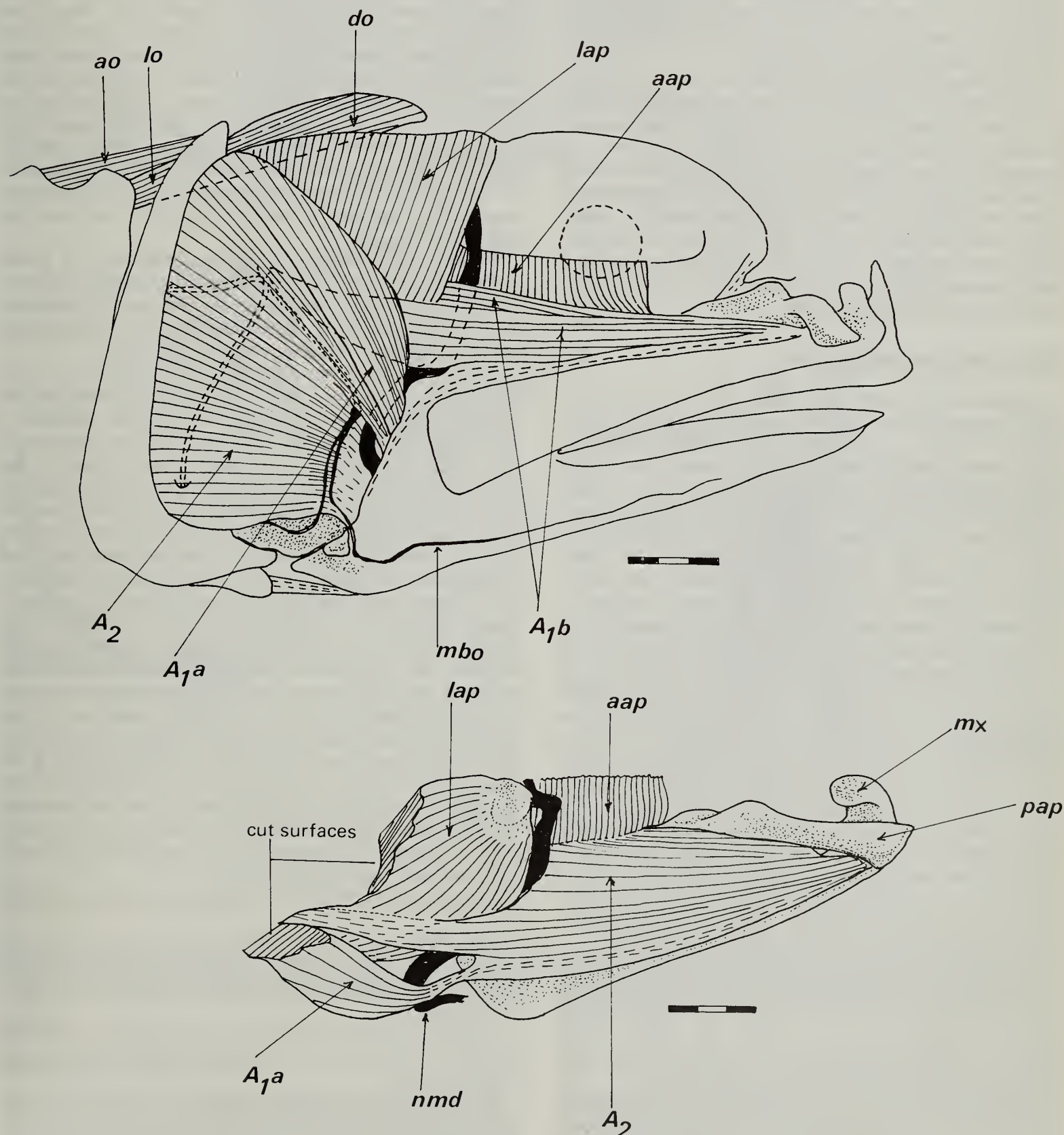
Fig. 28 Facial muscles and nerves of *Spectrunculus grandis*. Above, right lateral view; below, dorsal view of right muscle A1b showing its relationships with surrounding musculature. Nerves and medial extent of muscles indicated respectively by short and long dashed lines.

part of the adductor muscle which lies medial to the mandib-ularis nerve and inserts on the lower jaw is regarded as A2 (Fig. 27). As in gadiforms, muscle A1b lies lateral to the ramus mandibularis, or at least its outer division does; the divided 'A1b' of ophidiiforms appears to be synapomorphic for the group. A similar modificiation of 'A1b' is a diagnostic character of supragadoids (*sensu* Howes, 1991b) where 'A1b' lies entirely medial to A2 (Howes, 1988). *Acanthonus* dis-plays a secondarily derived condition in having only an outer segment of A1b, the inner having been lost. The backward looping of the ramus mandibularis around muscle A1b in *Ophidion* (Howes, 1988: 35, Fig. 23A) sets this genus apart from other ophidiiforms examined.

In *Acanthonus* the *dilatator operculi* (do, Fig. 27) is exten-sive and occupies a cranial fossa in the pterotic and posterior part of the sphenotic. It is not covered by the *adductor mandibulae* or LAP muscles. In all other ophidiiform taxa examined, with the exception of two (see below) the DO runs behind the adductor and LAP muscles and originates from a narrow pterotic fossa situated on either the lateral or ventro-lateral surface of the bone (Fig. 28, top). Only in *Tauredo-phidium* and *Xyelacyba* is the DO expanded and lies in a dorsally situated fossa and in the former the muscle is even more extensive than in *Acanthonus*.

Pelvic girdle and innervation

In ophidiiforms the pelvic girdle, when present, is reduced to a small triangular bone (in the Carapidae examined it is a slender rod with a cartilaginous anterior tip sandwiched between the tips of the horizontal cleithral limbs, making it in effect, a ventral appendage of the pectoral girdle (Fig. 29B). The anterior shift of the pelvic girdle has also involved modification of the muscles and nerves which motivate the pelvic fin rays. The *sternohyoideus* muscle, as in other teleosts, runs from the lower part of the cleithrum and inserts along the urohyal, but unlike the common situation, a ventromedial segment detaches completely or partially from the main body of the muscle, and its ventral attachment is to the cleithral symphysis above the pelvic bones (Fig. 29A). In most ophidiiforms the posterior border of the urohyal is near to the cleithral anterior margin and the medial segment of the *sternohyoideus* lies, for the most part, between the two outer segments. In *Acanthonus*, however, the urohyal is reduced in size and widely separated from the cleithrum and the medial segment of the *sternohyoideus* is well-separated from the lateral elements which extend further posteriorly along the cleithral limb (Fig. 29A). The pelvic muscles are restricted to the pelvic bone and lack any connection with the *sternohyoi-deus*. Hypaxial muscle runs forward between the cleithra and attaches to their medial walls; the *infracarinalis anterior* also extends forward to attach to each pelvic bone (Fig. 29C).

Other than *Acanthonus*, the distinct separation of the medial section of the *sternohyoideus* is present only in *Hoplo-brotula*, *Sirembo* and *Dicrolene* (all members of the ophidiid subfamily Neobythitinae *sensu* Cohen & Nielsen, 1978) whereas in *Brotula* (Brotulinae) it is integrated to the same degree as in other neobythitines (i.e. *Bassozetus*).

The situation in *Genypterus*, *Lepophidium* and *Ophidion* (all members of the Ophidiinae *sensu* Cohen & Nielsen, 1978) is more complex than in other ophidioids. Cohen & Nielsen (1978) recognised the subfamily Ophidiinae princi-pally on the possession of a modified cleithrum where the horizontal limb extends forward as a bony filament, thus

advancing the pelvic girdle which is supported between the cleithral extensions. It should be noted that it is the medial bony laminae of the cleithra which extend forward and the cleithral tips remain in the approximate position of those of other ophidiiforms, *viz* beneath the basioccipital, but instead of meeting symphyseally they diverge and are connected in the midline only by hypaxial musculature. Although Cohen & Nielsen (1978) show the pelvic girdle sandwiched between the extended laminae, in the taxa examined here the cleithral bar attaches ligamentously to the pelvic bone (cle, Fig. 30). The *sternohyoideus* muscle is distally divided into lateral and medial portions. The majority of the posterior fibres of the lateral section attach to the urohyal while the ventral fibres converge into a tendon which attaches to the base of the urohyal; the medial portion runs directly to the inner face of the pelvic bones. The urohyal is extensive and canopy-like, forming a cover above the medial section of the *sternohyoi-deus* (ut, Fig. 30B); posteriorly the urohyal is firmly attached to the cleithral limbs by the *sternohyoideus*; anteriorly it attaches by a ligament to the 2nd hypohyal as well as to the ventrohyal (Fig. 30A).

Of the taxa examined, *Lamprogrammus* lacks a pelvic girdle and consequently any medial division of the *sternohyoi-deus* (Cohen & Rohr, 1992 detect the presence of a rudimen-tary pelvic girdle in *L. shcherbachevi*); the *supracarinalis anterior* attaches to the inner cleithral symphysis.

The innervation of the ophidiiform pelvic girdle has been described by Freihofer (1970) in *Brotula* and *Ogilbia* and by Machida (1988) for *Neobythites*. Both authors describe a hypertrophied branch of the ramus lateralis accessorius (RLA-PP) exiting from the posterodorsal region of the cranium and following a path along the posterior margin of the cleithrum which turns mesad and meets the third ventral spinal nerve (VSR3) to enter the two pelvic fin rays. In *Brotula*, *Hoplobrotula*, *Sirembo*, *Dicrolene*, *Bathyonus* and *Spectrunculus* the RLA-PP nerve crosses from the cleithrum to the pelvic bone *beneath* the hypaxial muscle, making it readily visible when the skin is removed (Fig. 30D). Each VSR3 descends to the ventral midline to run together between the *infracarinales anteriores* before meeting the RLA-PP. In the ophidiines *Ophidion*, *Genypterus*, *Parophid-ion* and *Lepophidium*, the nerve course is similar except that the RLA-PP and VSR3 pass together between the cleithral limbs and beneath the canopy-like urohyal (Fig. 30). In all other taxa examined (including *Ogilbia* and *Neobythites*) the RLA-PP is relatively thin, passes mesad to the cleithrum and hypaxial muscles and meets the vsr3 directly above the pelvic bone, both nerves exiting together between the *infracarinales anteriores* and entering the pelvic rays.

In summary, the respective conditions in the taxa examined are:

RLA-PP hypertrophied, running close to cleithral border and exposed laterally and ventrally, joining VSR3 posteri-orly: *Brotula*, *Hoplobrotula*, *Sirembo*, *Dicrolene*, *Bathyonus*, *Spectrunculus*.

As above but RLA-PP and VSR3 running together through modified cleithrum and urohyal: *Ophidion*, *Genypterus*, *Lepophidium*.

RLA-PP thin, not exposed laterally or ventrally, joining VSR3 anteriorly: *Acanthonus*, *Abyssobrotula*, *Aphyonus*, *Barathronus*, *Bassozetus*, *Brosmophyciops*, *Cataetyx*, *Dipla-canthopoma*, *Glyptophidium*, *Hypopleuron*, *Lamprogram-mus*, *Lucifuga*, *Monomitopus*, *Neobythites*, *Ogilbia*, *Penopus*, *Porogadus*.
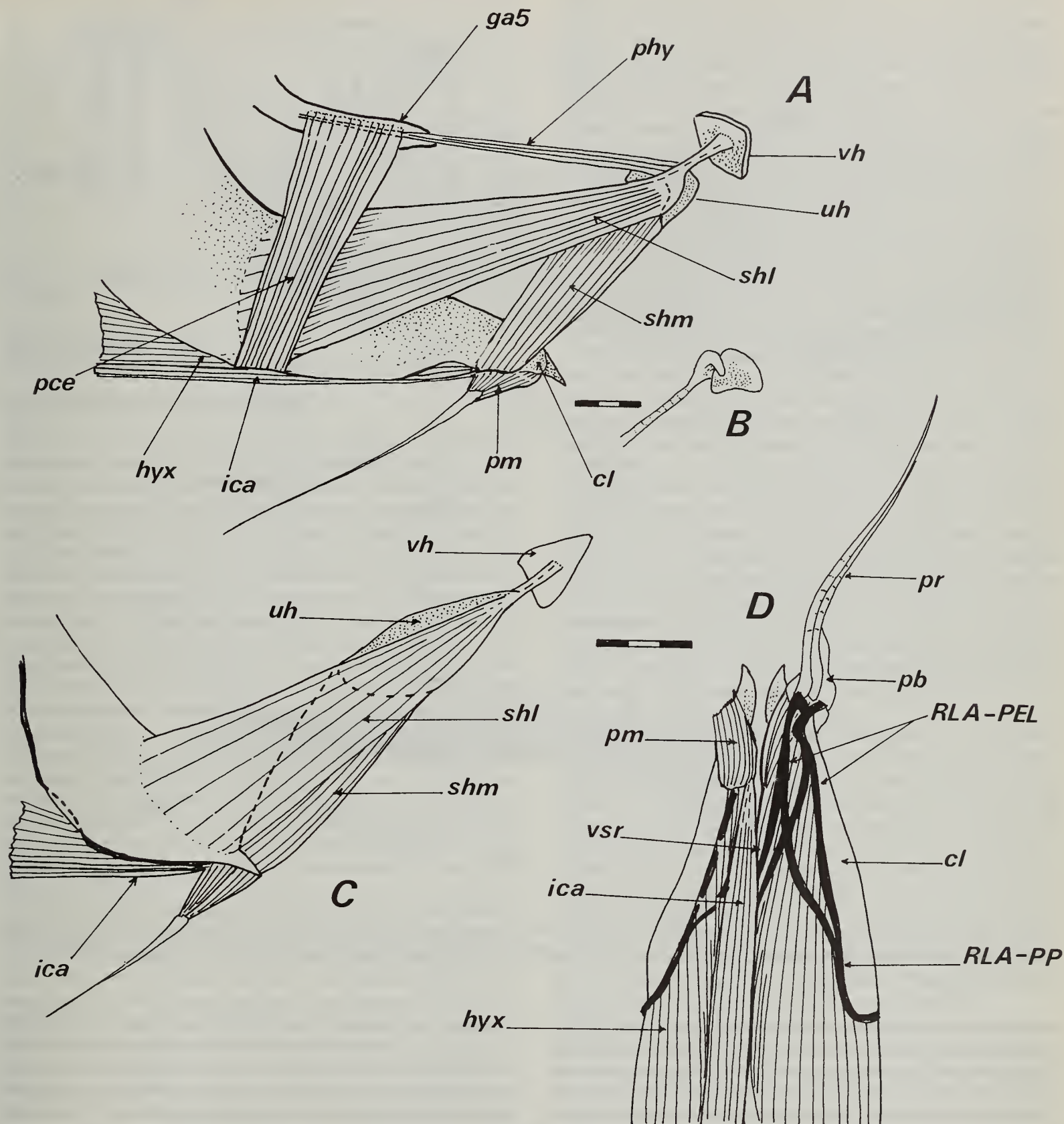
Fig. 29 Pectoral-pelvic girdle associations. A, *Acanthonus armatus*, right lateral view showing principal muscles. B, isolated pelvic bone with fin ray attached. C, *Bassozetus* sp., right lateral view of *sternohyoideus* muscle (dashed lines show limits of the medial part of the muscle and lower border of the urohyal). D, *Spectrunculus grandis*, ventral view; *infracarinalis anterior* removed from left side of fish to display nerves.

Pharyngohyoideus muscle

In all ophidiiforms and carapids examined the *pharyngohyoideus (rectus communis)* muscle extends from the urohyal to the fifth gill-arch (Fig. 29A). In the majority of taxa it runs from the anterodorsal tip of the urohyal and connects both elements with no intermediate attachment but in *Monomitopus* and *Neobythites* it also attaches to the third hypohyal and

in *Spectrunculus* to the fourth. In the ophidiines *Ophidion*, *Genypterus* and *Lepophidium*, the *pharyngohyoideus* is a broad band-like muscle extending posteriorly from the face of the urohyal and attaching ligamentously to the fourth gill-arch as well as the fifth.

Howes (1988) noted that in gadoids and a few macrouroids *pharyngohyoideus (rectus communis)* attaches directly to the
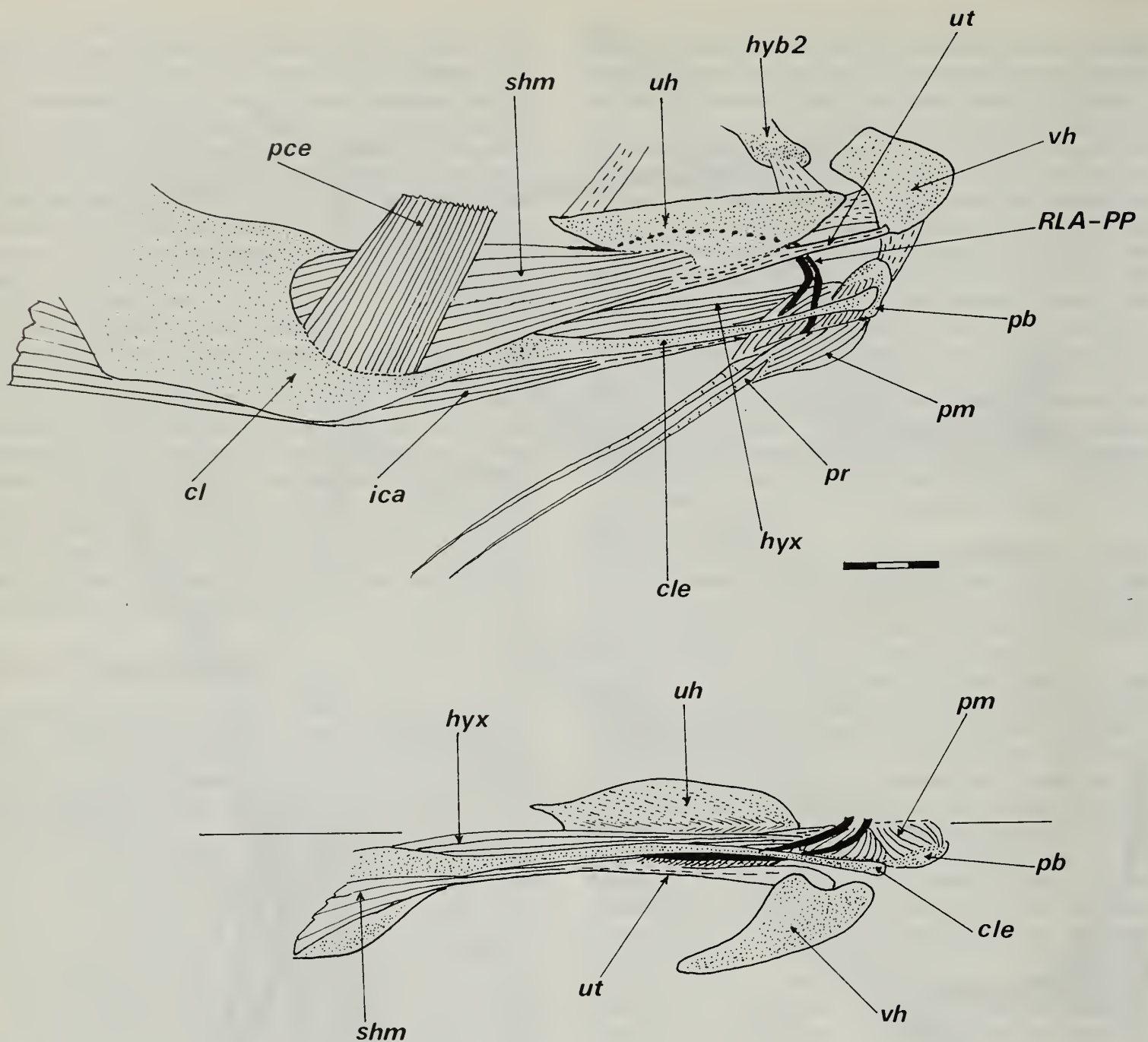
Fig. 30 *Genypterus blacodes*, pelvic girdle anatomy. Above, right lateral; below, ventral view. In the lateral view, the course of the RLA-PP nerve beneath the urohyal is indicated by a broken line. In the ventral view the muscles and nerves of the specimen's right side have been removed to expose the urohyal.

anterodorsal tip of the urohyal or *via* the *sternohyoideus* (as in ophidiiformes and carapids) whereas in most macrouroids it attaches to the bone's lateral face. The *sternohyoideus* mediated condition of the *pharyngohyoidus* in gadoids and some macrouroids was considered by Howes (1988) as having been derived from direct attachment to the urohyal keel, the (derived) acanthomorph state. In the group of ophidiform genera which possess the latter condition (ophidiines) there is no median keel, but merely a dorsal ridge so that the muscle inserts on the canopy-like base-plate of the bone (see above). Thus, the condition in ophidiines is considered to have been independently derived from that in other acanthomorphs.

Anterior mandibular pores

Acanthonus, in common with 50% of ophidiiform genera examined has a single opening in the dentary close to the symphysis which is the anterior opening of the mandibular

sensory canal. In the other 50% of taxa there is an additional opening on the medial rim of the dentary, posterior to the ventral symphyseal opening. The medial aperture opens into the cleft where the isthmus (*protractor hyoideus* muscle) joins the dentary symphysis and is often covered by a fold of skin extending along the medial rim of the dentary (in *Dinematichthys* there are separate flaps of skin covering the medial openings). In *Spectrunculus*, *Monomitopus*, *Diplacanthopoma*, *Ogilbia*, *Dinematichthys* and *Lucifuga* the medial opening is large and in the latter three genera the dentary rim is notched at the medial opening (med, Fig. 31A). In *Sirembo*, *Hoplobrotula*, *Ophidion*, *Lepophidium* and *Genypterus* the medial opening is small and narrowly separated in the midline from its antimere (Fig. 31B) but in *Porogadus* and *Tauredophidium* the medial openings are extensive and widely separated. In *Brotula* the so-called barbels are tubular extensions of the medial openings which communicate directly with the mandibular canal.
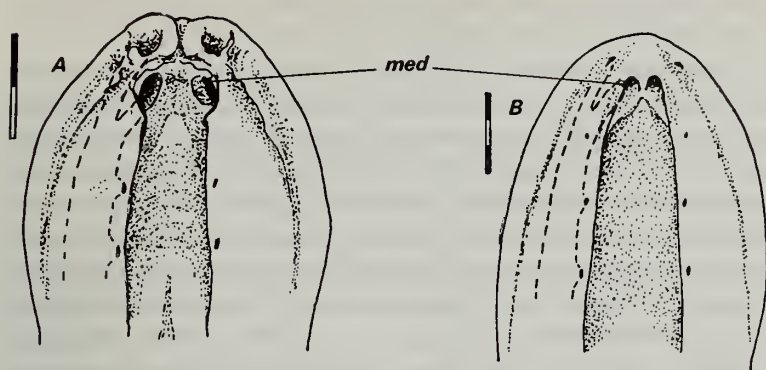
Fig. 31 Mandibular pores of A, *Ogilbia cayorum*; B, *Sirembo imberis*.

DISCUSSION

Specializations of *Acanthonus*

Acanthonus possesses a series of uniquely derived inter-linked osteological, myological and neurological cranial features. It has a lower jaw-palatine bite, a consequence of the lateral shift of the palatopterygoid articulation by outward curvature of the quadrate, in turn laterally shifted through outward curvature of the dorsal region of the hyomandibular. The relocation of the anterior hyomandibular strut has necessitated the hyomandibularis nerve piercing the anterior lamina of the bone rather than the strut itself. The preoperculum gives additional rigidity to the quadrate by its widened horizontal limb. The loss of upper jaw biting strength is reflected in the reduction of adductor muscle A1b whereas the increased importance of lower jaw-opercular series coupling is reinforced by hypertrophy of the *dilatator operculi* muscle.

Howes (1989) hypothesised that the loss of a trigeminal chamber in gadiforms was a response to increased buccal expansion so giving more freedom of passive movement to the nerve tracts. That hypothesis is here extended to the similar condition in *Acanthonus* where expansion of the buccal cavity is indicated and also accompanied by loss of a trigeminal chamber.

Nielsen (1966) commented on the biology of *Acanthonus* and examined stomach contents of six specimens, the majority of which contained crustaceans and dorsal filt of polychaetes. Another specimen, however, contained bones of a conspecific. In the three specimens here examined (310, 290, 240 mm TL) the stomach contents contained a 'mush' in which only crustacean elements are discernible.

Horn *et al.* (1978) reported on the large size of the cranial cavity of *Acanthonus* and the fact that it was filled with a low-density fluid. The authors hypothesised that since the head is the heaviest part of the body, the concentration of positively buoyant fluid provides lift and allows the fish to maintain a horizontal position with minimum swimming energy. Horn *et al.* suggest that the head might function as an acoustic dome. Certainly the cranial wall is exceedingly thin and the labyrinth is, compared with other ophidiforms (and gadiforms), extensive (Fig. 11). The fluid in which the brain is bathed is retained in the cranium by the membrane covering the large common optic-olfactory-trigeminal opening.

Compared with other ophidiiforms *Acanthonus* appears to have a relatively poorly developed olfactory system, the olfactory tract being thin and the nasal rosette having only five or six lamina (cf. 8–18 in other taxa examined (Fig. 32A).

Only *Tauredophidium* and *Typhlonus* have reduced nasal rosettes with six laminae (Fig. 32B). In nearly all the specimens of *Acanthonus* available the nasal rosette is missing; since it is small and firmly attached to the connective tissue surrounding the nasal opening it appears to have become detached with the skin during collecting (the specimens are all badly damaged). In the two type specimens of *A. armatus* the rosettes are clearly visible in only one specimen (BMNH 1967.18.7:58). In the type specimen of *Typhlonus nasus* the nasal rosette is attached to and surrounded by fatty tissue. In *Xyalecyba* the nasal 'rosettes' appear to be in the form of three pear-shaped plates. Of the other taxa examined most have large nasal rosettes bearing ten–twelve laminae (Fig. 32C), *Monomitopus* and *Genypterus* both have eighteen and *Spectrunculus* has in excess of twenty (Fig. 32D), *Dicrolene* and *Glyptophidium* have the lowest number, *viz* eight.

Compared with most other ophidiiforms the eyes of *Acanthonus* are small (9.1–9.7% of head length) and the *recti* muscles are thin (Fig. 27); the lens is large and surrounded by a ring of pigment. Of 23 genera in which the eye/head length proportion has been calculated, only three approach the ratio of *Acanthonus*: *Genypterus, Dinematichthys* and *Tauredophidium*. In the two former genera the ratio is equal to or slightly less than that of *Acanthonus*, respectively, 6.8–8.2 and 9.0–9.8% of head length. The relatively small ratio in *Genypterus* is a reflection of its disproportionately elongate skull due to the lengthened parasphenoid ascending process and pterosphenoid (Fig. 10A). *Tauredophidium* has an eye diameter/head length ratio of 5.0% (the eye is covered with skin). In the majority of genera the proportional range is 10.3% (*Sirembo*) – 24.6% (*Lepophidium*); mode, 20.9% of head length. This range includes *Xyelacyba* (12.5 & 13.9% in the two specimens measured).

Scales are lacking in all six specimens of *Acanthonus* examined but according to Nielsen (1966), small, thin, cycloid scales occur on the head and body. Mats of sponge spicules were found associated with all the specimens, in the orbital cavities, gill chambers and mouths. The spicules apparently belong to a hexactinellid of the family Pheronematidae which tend to carpet extensive areas of the substrate in parts of the north Atlantic; these sponges play host to many invertebrates (S. Stone, pers. comm.). It is perhaps not an artefact of capture that the fishes are covered with sponge spicules but that they actively feed within the sponge beds and even bite through the sponge basket, which may be one explanation for the derived palatine-lower jaw bite.

Horn *et al.* (1978) surmise that *Acanthonus* conforms to Childress & Nygaard's (1973) hypothesis that deep-sea fishes conserve energy and discourage predation. They point out that the enlarged head of the fish and a correlated large mouth allow a wide size-range of prey. It does not necessarily follow that an expanded mouth is a correlate of an enlarged cranium (cf. the large-headed, small-mouthed macrouroids, *Echinomacrurus* and *Squalogadus*) and in *Acanthonus* it is not simply the capacity of the mouth but its derived function (lower jaw-palatine bite) which presumably further widens its prey spectrum (see above).

Relationships of *Acanthonus* and the classification of ophidiiforms

Cohen & Nielsen (1978) placed *Acanthonus* in the neobythitine tribe Sirembini along with *Sirembo, Hoplobrotula,*

Tauredophidium, Dannevigia and *Xyelacyba*. Of these genera I have examined all except *Dannevigia* and find that *Tauredophidium* and *Xyelacyba* are closest to *Acanthonus* in overall morphology with a long, stout ventroposterior preopercular spine, a preopercular-opercular ligament covering the articulation of the operculum, a narrow operculum, occlusion between the palatine and lower jaw teeth and a 'platform' articulation between the preoperculum and quadrate and narrow operculum. *Tauredophidium* also possesses a short, single ethmoid spine (contrary to Cohen & Nielsen, 1978) but a spine is lacking in *Xyelacyba*. A superficial and radiographic examination of *Xyelacyba* suggests that although lacking an ethmoid spine it more closely resembles *Acanthonus* than does *Tauredophidium* in the morphology of its suspensorium, palatoquadrate and the first neural arch. *Hoplobrotula* also possesses an ethmoid spine (Machida, 1990), lacking in *Sirembo*, but both share an almost identical pelvic-hyoid morphology where the medial section of the *sternohyoideus* is well-separated from the lateral parts and the urohyal is reduced to a small triangular element. These are also specialized characters possessed by *Acanthonus*. Despite these apparent synapomorphies I would agree with Cohen & Nielsen's (1978) doubt that their Sirembini is a natural assemblage, since *Acanthonus* lacks the synapomorphic condition of the RLA-PP of *Sirembo* and *Hoplobrotula* and also possesses the derived external branching of the supraorbital trunk of the trigeminal nerve.

The other neobythitine division, Neobythitini, was characterized by Cohen & Nielsen (1978) solely on the basis of pelvic fin position (at the level of the preoperculum) and it includes *ca* 30 genera of which 12 have been examined. None of the characters reviewed here appear to be synapomorphic for this sample of genera and it seems unlikely that the Neobythitini as presently construed is monophyletic.

The characters described above and the limited number of taxa examined do not permit an in-depth evaluation of the existing classification of ophidiiforms (Cohen & Nielsen, 1978). They certainly uphold the division of Ophidiinae and Brotulinae. Modification of pelvic and pectoral girdle structure, associated musculature and innervation, urohyal morphology and swimbladder-vertebral association characterize the former group (six of the eight included genera have been examined). The path of the hyoideus branch of the facial nerve through the hyomandibular characterizes the Brotulinae (*Brotula* only). The Brotulinae shares derived features with several other taxa, e.g. narrow optic-olfactory foramen and separate medial section of *sternohyoideus* muscle with *Hoplobrotula*, *Sirembo* and *Dicrolene*, and hyomandibular flange for hyoideus branch of VII with the former; frontals contacting the pterosphenoid with *Sirembo* and *Dinematichthys*; and forward position of the forebrain with *Monomito-*

pus (the latter is most likely a convergent character since both taxa have short neurocrania).

Cohen & Nielsen (1978) established a classificiation of ophidiiforms in which two orders, Ophidioidei and Bythitoidei were distinguished primarily on their respective oviparity and viviparity and secondarily on the position of the anterior nostril, either well or just above the upper lip. As pointed out by Patterson & Rosen (1989) the bythitoid characters are probably apomorphic, whereas the ophidioid ones are plesiomorphic. Within the Ophidioidei were included the Carapidae and Ophidiidae. The former have been dealt with most recently by Markle & Olney (1990) who have discovered synapomorphies which reaffirm the family's monophyly. These authors did not specifically address the problem of carapid relationships and merely point out that the Carapidae does not appear as '. . . an obvious sister group' to any other ophidiiform lineage. The Carapidae appear to be the sister-group to other ophidiiforms on the basis of their possessing a smaller, shallower exoccipital but which, like other ophidiiforms excludes the supraoccipital from the foramen magnum. Like brotulines, some neobythitines and ophidiines, carapids possess enlarged anterior epipleural ribs, similarly modified swimbladders and a well-developed basioccipital cavity with a corresponding ventromedial process on the first centrum; paired ventro-lateral processes on the lateral ethmoid articulating with the palatine, all features which characterise Ophidiiformes.

The Ophidiidae are diagnosed by Cohen & Nielsen (1978) on two plesiomorphic features: a supramaxilla and presence of body scales and on the dorsal fin rays being equal to or longer than the anal rays. This latter feature was used principally to distinguish the Ophidiidae from the Carapidae but as equal length dorsal and anal fin rays occur amongst bythitoids it is not a diagnostic character.

Of their four subfamilies the Ophidiinae and Brotulinae are clearly united on shared anatomical features of the pectoral girdle and hyoid musculature (Cohen & Nielsen, 1978; this paper). The other two subfamilies are Brotulotaeniinae, characterized by derived squamation and spinous gill-rakers (in other osteological characters it appears plesiomorphic) and Neobythitinae, diagnosed on plesiomorphic features (i.e., absence of ophidiine characters).

The Bythitoidei comprises two families, Bythitidae and Aphyonidae, the latter characterized by absence of scales and swimbladder, reduced eyes and other generally neotenic features. The Bythitidae comprises two subfamilies, Bythitinae and Brosmophycinae recognised respectively by the continuity or separation of the caudal with the dorsal and anal fins. Part of the Brosmophycinae (recognised as a tribe, Dinematichthyini) seems well characterized by a synapomorphic intromittent organ (in males) having 'ossified' elements. Of the two members of the Brosmophycini examined, *Brosmophyciops* is most like the Dinematichthyinae in its anterior vertebral column and swimbladder morphology. *Lucifuga* does not, on the basis of its vertebral column-swimbladder anatomy, appear to be closely related to *Brosmophyciops*, nor for that matter, to the group which includes the deep-water taxa (Group 2 above). Of the characters discussed in this text, the Aphyonidae retain the plesiomorphic states. A swimbladder is absent, which must certainly represent secondary loss since it is present in virtually all other ophidiiforms. However, the derived morphology of the opercular and hyoid bones supports Cohen & Nielsen's (1978) recognition of aphyonid monophyly.
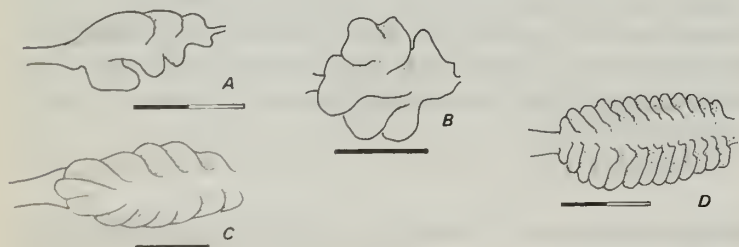

Fig. 32 Nasal rosettes of A, *Acanthonus armatus*; B, *Tauredophidium hextii*; C, *Ophidion rochei*; D, *Spectrunculus grandis*. Viewed as *in situ*, posterior to the left.

In the three aphyonid genera examined, *Aphyonus, Barathronus* and *Nybelinella*, the interoperculum is reduced to a narrow strip of bone having nearly the same width as the ligament connecting it to the mandible (Fig. 33). The interopercular-mandibular ligament is elongate, twice or more the length of that in other ophidiiforms (cf. Fig. 33B). Posteriorly, the interoperculum is connected to the interhyal by connective tissue and a short, strong ligament. Distally, the interhyal is also syndesmotically connected to the tip of the posterohyal and the entire junction of the posterohyal-interhyal-interoperculum is wrapped in thin connective tissue; proximally the interhyal is attached to the posterior medial border of the preoperculum (Fig. 33A). The suboperculum is also apparently reduced but its shape cannot be readily discerned in the non-cleared and stained specimens dissected. In all these features aphyonids differ from other ophidiiforms where the interoperculum is deep, triangular or boomerang-shaped; the interopercular-mandibular ligament short and the interhyal distally connected with the posterior half of the interoperculum and with the posterohyal, and proximally attached to the central region of the preoperculum (Fig. 33B).

The majority of ophidiiform taxa are contained in the non-monophyletic Neobythitinae and Bythitidae, the former containing *ca* 50 genera, the latter *ca* 28 (Cohen & Nielsen, 1978). According to Patterson & Rosen (1989) these two assemblages could be distinguished on the basis of differences in their cranial-vertebral articulation, that of bythitids being derived. As discussed above (p. 111) this is a doubtful synapomorphy and is not supported by the synapomorphies identified here (hypertrophy of the RLA-PPD nerve (p. 122), branching of the supraorbital trigeminal trunk external to the trigeminal foramen (p. 104), and vertebral-swimbladder interconnections). These features also support a major dichotomy of ophidiiforms but different to that proposed by Patterson & Rosen (1989); Table 1.

Those taxa (except for two, see below) with the derived form of RLA-PPD (Group A) have the plesiomorphic, internal branching of the superficial-trigeminal nerve trunks while those with the derived external branching pattern (Group B) possess the plesiomorphic pelvic nerve condition. Taxa of Group A comprise the Ophidiinae (*sensu* Cohen & Nielsen, 1978) and Brotulinae (*Brotula*). The 'neobythitines' *Hoplobrotula, Sirembo, Neobythites* and *Dicrolene* display an intermediate connection of nerve branching (p. 105) and *Hoplobrotula, Sirembo* and *Dicrolene* also share derived features which indicate that they form a monophyletic group
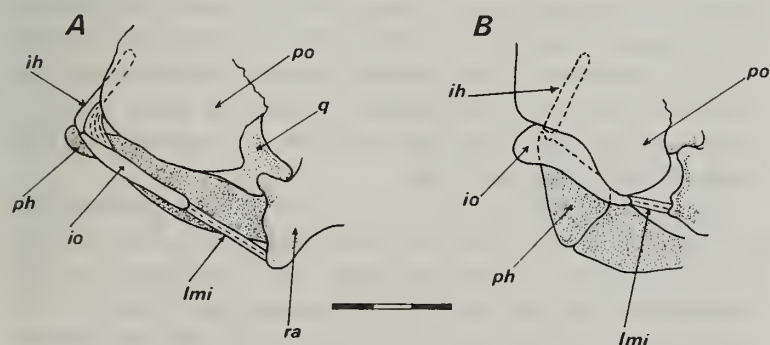
Table 1 Group membership of the genera examined. **Group A.** RLA-PP nerve hypertrophied, exposed laterally and ventrally; some taxa with modified cleithrum and urohyal; supraorbital trunk of trigeminal primitively dividing within the cranium; anteromedial mandibular pore openings small. **Group B,** RLA-PP normal; cleithrum and urohyal unmodified; supraorbital trunk of trigeminal dividing external to facialis foramen; anteromedial mandibular pore openings usually large. **Group 1,** swimbladder anteriorly situated, intimately associated with expanded first-third (epipleural) ribs the first of which occurs on the first centrum, swimbladder often with modified anterior cap and with muscle attachment; first neural arch short. **Group 2,** swimbladder posteriorly situated, not associated with anterior ribs which are unexpanded, the first of which occurs on the third centrum (pleural); swimbladder not modified but with muscle attachment; first neural arch reduced and autogenous.

Abbreviations: X = 'intermediate' condition; O = features of these groups absent; ? = condition unknown. Under 'Present classification', A = Aphyonidae, B = Bythitoidei, N = Neobythitinae, O = Ophidiidae.

Groups	A	B	1	2	Present classification
Abyssobrotula		+		+	N
Acanthonus		+		+	N
Barathrodemus		+		+	N
Bassozetus		+		+	N
Bathyonus	+	+		+	N
Brosmophyciops		+	+		B
Brotula	+		+		O
Cataetyx		+		+	N
Cherublemma	+		+		O
Dicrolene	X	X	+		N
Diplacanthopoma		+		+	B
Genypterus	+		+		O
Glyptophidium		+	+		N
Hoplobrotula	X	X	+		N
Hypopleuron[1]	+	+	+		N
Lamprogrammus		+	+		N
Lepophidium	+		+		O
Lucifuga		+	X	X	B
Monomitopus		+	+		N
Neobythites	X	X	+		N
Ogilbia		+	+		B
Ophidion	+		+		O
Parophidium	+		+		O
Petrotyx	?	?	+		N
Penopus		+		+	N
Porogadus		+		+	N
Pycnocraspedum	?	?	+		N
Sirembo	X	X	+		N
Spectrunculus	+	+		+	N
Aphyonidae:					
Aphyonus	O	O	O	O	A
Barathronus	O	O	O	O	A

[1] *Hypopleuron* has a normal RLA-PP and the supraorbital trunk divides primitively within the trigeminal chamber so that although the taxon belongs to Groups A and B it lacks the derived features of those groups.

Fig. 33 Interoperculum and its associations in A, *Barathronus bicolor* (dissected specimen, lateral view); B, *Monomitopus metriostoma* (cleared and stained specimens, right lateral view).

(Fig. 34). In turn they share a similar, apparently derived, mandibular sensory canal pore pattern with ophidiines (p. 126). The taxa belonging to Group B contains those other taxa presently assigned to the Neobythitinae (of the Ophidiidae) and the Bythitidae.

The neobythitine *Hypopleuron* and the bythitoid Aphyonidae possess neither of these derived characters. Loss of epipleural ribs places the Aphyonidae with Group B taxa.
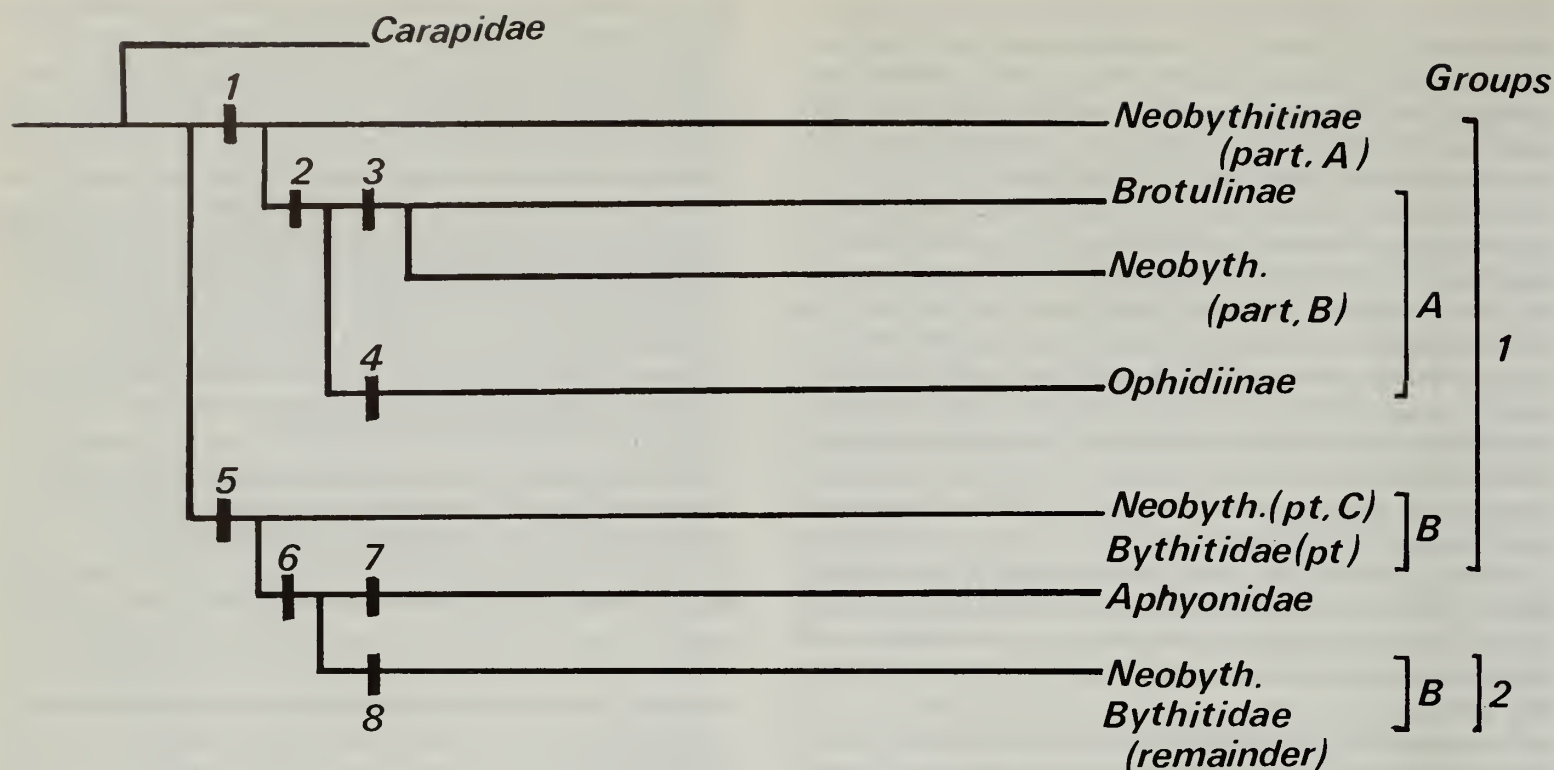
Fig. 34 Distribution of synapomorphies among investigated taxa and their correspondence with the groupings given in Table 1. The Carapidae are indicated as being the sister-group to other ophidiiforms on the basis of their sharing an enlarged exoccipital which excludes the supraoccipital from the foramen magnum but which still allows the dorsal part of the supraoccipital to form the posterior margin of the skull. They also share the ophidiiform features of expanded anterior ribs, modified swimbladder and associated muscles, basioccipital-vertebral articulation and well-developed paired lateral ethmoid facets (see text). **Synapomorphies:** 1) exoccipital dorsally expanded to exclude supraoccipital from forming the dorsoposterior cranial border; 2) RLA-PP nerve hypertrophied and exposed ventrally to hypaxial muscles; 3) olfactory-optic nerve foramen reduced to narrow aperture; separation of medial part of *sternohyoideus* muscle (occurs convergently in *Acanthonus*); enlarged mandibular sensory pores; 4) anteriorly extended cleithra; urohyal canopy-like with modified course of RLA-PP and VSR3 nerves; *pharyngohyoideus* muscle expanded; 5) supraorbital trunk of trigeminal nerve complex dividing externally to facialis chamber; 6) reduction or loss of anterior ribs; 7) opercular bones modified; 8) first neural arch reduced and autogenous; swimbladder situated posteriorly.

Neobythitinae (part A) = *Hypopleuron*; (part B) = *Hoplobrotula, Sirembo, Dicrolene*: (part C) = *Monomitopus, Lamprogrammus, Glyptophidium*; Bythitidae (part) = *Brosmophyciops*.

Groups 1 and 2 characterised on the basis of (divergently) derived swimbladder-vertebral connections correspond for the most part with the A and B groupings. Most taxa of Group 2 also belong to Group B and an overlap between Groups 1 and B occurs only amongst five genera, *biz. Brosmophyciops, Glyptophidium, Lamprogrammus, Monomitopus* and *Ogilbia* (Table 1). Membership of both Groups A and B is restricted to two genera, *Bathyonus* and *Spectrunculus*. Both possess the respective derived conditions of these groups, namely, hypertrophy and ventral exposure of RLA-PP nerve and external division of the supraorbital trunk of the trigeminal complex. Both are also members of Group 2 having the derived conditions of rib loss and posterior placement of the swimbladder. Since these genera lack any synapomorphies which characterise ophidiines, brotulines and the few 'neobythitine' genera included in Group A, it must be assumed that the RLA-PP nerve characters have been evolved independently. The division between ophidiods and bythitoids made by Cohen & Nielsen (1978) on the basis of ovo- and viviparity is transgressed by two genera, *Brosmophyciops* and *Ogilbia* both of which, by virtue of their anteriorly situated swimbladder and expanded ribs belong to Group 1. These and the aphyonids apart, the viviparous taxa are included within that assemblage possessing external branching of the supraorbital-trigeminal nerves, namely, Group B.

The 'neobythitine' *Hypopleuron* stands phylogenetically apart from other taxa in lacking any of the synapomorphies recognised here. The majority of taxa referred to the Neobythitinae and Bythitidae belong to a derived assemblage whose sister-group is the Aphyonidae, characterised by mostly reductive features (see above). The distribution of synapomorphies and their correspondence with the groups recognised above as A, B, 1 and 2 are shown in Fig. 34.

As an aside, it may be pointed out that the arrangement of caudal fin muscles in ophidiiforms correspond more closely to those of pediculate paracanthopterygians and acanthopterygians than to gadiforms. Howes (1991a) noted that gadoids have 'reduced' caudal muscles insofar as a superficial *interradiales, hypochordal longidorsalis, flexores dorsales* and *ventrales* are lacking. Ophidiiforms possess all these muscles, albeit that the superficial *interradiales* are reduced to a thin band of widely spaced fibres.

Regrettably, this study has not conclusively resolved the phylogenetic relationships of *Acanthonus* but available character data from *Tauredophidium* and *Xyelacyba* (p. 128) suggest that the three taxa form a monophyletic group. As yet the anatomy of *Tauredophidium* and *Xyelacyba* is too imperfectly known to resolve the trichotomy. The shared features of hyoid muscle anatomy and an ethmoid 'spine' which indicate relationship of *Acanthonus* and *Tauredophidium* with *Hoplobrotula* and *Sirembo* are doubtful in the light of

the distribution of the trigeminal and pelvic nerve characters. No synapomorphy has emerged from this study which can further distinguish separate groups from within the larger body of taxa (in terms of the number investigated here) placed in Groups B and 2 (Fig. 34).

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